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Identification of New World aquatic invertebrate illustrations in *The Drake Manuscript*

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Images of aquatic invertebrates are included in a late 16th-century work, *Historie Naturelle des Indes*, also known as *The Drake Manuscript*. While the renderings are often whimsical and exaggerated, they nonetheless appear to be based on direct observations. We sought to identify these aquatic invertebrates and explore their early history. Most were identifiable to species based on the renderings and captions. Images of horseshoe crab were also found in *Brief and True Report of the Found Land of Virginia* (1590), which contains etchings derived from watercolours by John White. We speculate that renderings of horseshoe crab in *The Drake Manuscript* may have descended from a lost detailed watercolour by John White in connection with his voyages to Roanoke rather than being based on direct observations. Finally, the freshwater unionoid mussel illustration appears to be the oldest known depiction of mantle lures unique to some species in this taxon.

Keywords: Bivalvia; horseshoe crab; *Limulus polyphemus*; Mollusca; Unionoida

Introduction

Modern ecology and evolutionary biology are heavily steeped in the natural history reflections and reports contributed by highly visible naturalists such as Jean-Baptiste Lamarck (1744–1829), Alexander von Humboldt (1769–1859), and Charles Darwin (1809–1882). In addition to these and other highly noted naturalists, there also exist countless other renderings and descriptions by obscure, unknown, and/or amateur naturalists who, despite their lack of notoriety, nevertheless provide information that can be important for understanding the life history, ecology, and distributions of taxa prior to industrialization and globalization. An anonymous illustrated manuscript in French entitled *Historie Naturelle des Indes* dated to the late 16th century was published in 1996 by the Morgan Library and Museum in a facsimile edition entitled *The Drake Manuscript,* since there appears to be a connection with Sir Francis Drake's voyage to the New World (Janick 2012). The manuscript contains unpolished but lively watercolours of 62 botanical subjects; 89 renderings of fish, land and marine animals, and birds; and 43 illustrations of the activities of indigenous peoples of the Americas, Spaniards, and African slaves (Schwerdt 1928; Lestingant 1994; Klinkenborg 1996; Janick 2012). The manuscript also contains illustrations of aquatic invertebrates captured from waters of the Caribbean, the western Atlantic Ocean along the shores of what is now the United States of America (US), and freshwater rivers of the southeastern US, including a lobster, several bivalve molluscs (some of

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which are referred to as 'conches'), and two views of *Limulus polyphemus* horseshoe crab. Examination of these images suggests that they were based on observations of actual specimens despite the whimsical nature of some of the renderings (e.g. human-like eyes in the illustration of the lobster and the many serpent-like 'fish' associated with the stream-dwelling mussel). Our objective in this paper is to identify the species illustrated and comment on the origin of horseshoe crab illustrations in this and other contemporary printings of the late 16th and early 17th centuries. We also comment on the novelty of the freshwater mussel illustration as it relates to the history of the iconography for this taxonomic group.

Identification of aquatic invertebrates

Bivalve molluscs

Scallops

While several organisms designated as 'conches' in *The Drake Manuscript* are correctly identified as members of the Phylum Mollusca, they are bivalve molluscs (Class: Pelecypoda or Bivalvia), whereas contemporary conchs are univalve organisms in the Class Gastropoda. The bivalve molluscs rendered in illustration f. 43 are members of the contemporary Family Pectinidae (scallops) based on the watercolour illustrations, descriptions, and localities provided. The rendering in f. 43 (1 of 2) (Figure 1A) appears to be a single valve of *Nodipecten nodosus* lions-paw scallop. This species has a wide geographic distribution, from Cape Hatteras to Brazil, and also exhibits great phenotypic variability in colour (Abbot and Morris 1995). The red exterior colour with violet nacre is an especially favoured variation among shell collectors that is found within the location provided by the author (i.e. on the Guajire Peninsula in Colombia) (Table 1). The beak and umbo in the illustration are exaggeratedly bent and the hinge wings are disproportionately small but, given the coloration, locality, and general features of the illustration, the specimen was almost certainly *N. nodosus*. The rendering in f. 43 (2 of 2) (Figure 1B) is probably based on a specimen of *Lindapecten muscosus* rough scallop. While the illustration depicts only 17 transverse ribs versus the typical 20 or so described for the species (Abbot and Morris 1995), *L. muscosus* is characterized by the presence of erect scales or spines that make the external shell surface very rough, which is consistent with the description in *The Drake Manuscript* (Table 1).

Oysters

Illustration f. 57v (Figure 1C) appears to be a bivalve mollusc of the Family Pteriidae (pearl oysters). This illustration is very likely the artist's rendering of a specimen of *Pinctada imbricata* (Atlantic pearl-oyster). This species is highly variable in its appearance, often with concentrically arranged scaly projections that produce sculpturing on the shell surface (Abbot and Morris 1995). While such projections are not apparent in *The Drake Manuscript* rendering, they are not present in all specimens and may not have been a characteristic of the artist's specimen. The straight hinge line and highly flattened, nearly equal valves in *The Drake Manuscript* illustration are consistent with *P. imbricata*. However, the illustration clearly depicts a centrally located umbo and prominent concentric annuli. *Pinctada imbricata* typically has an

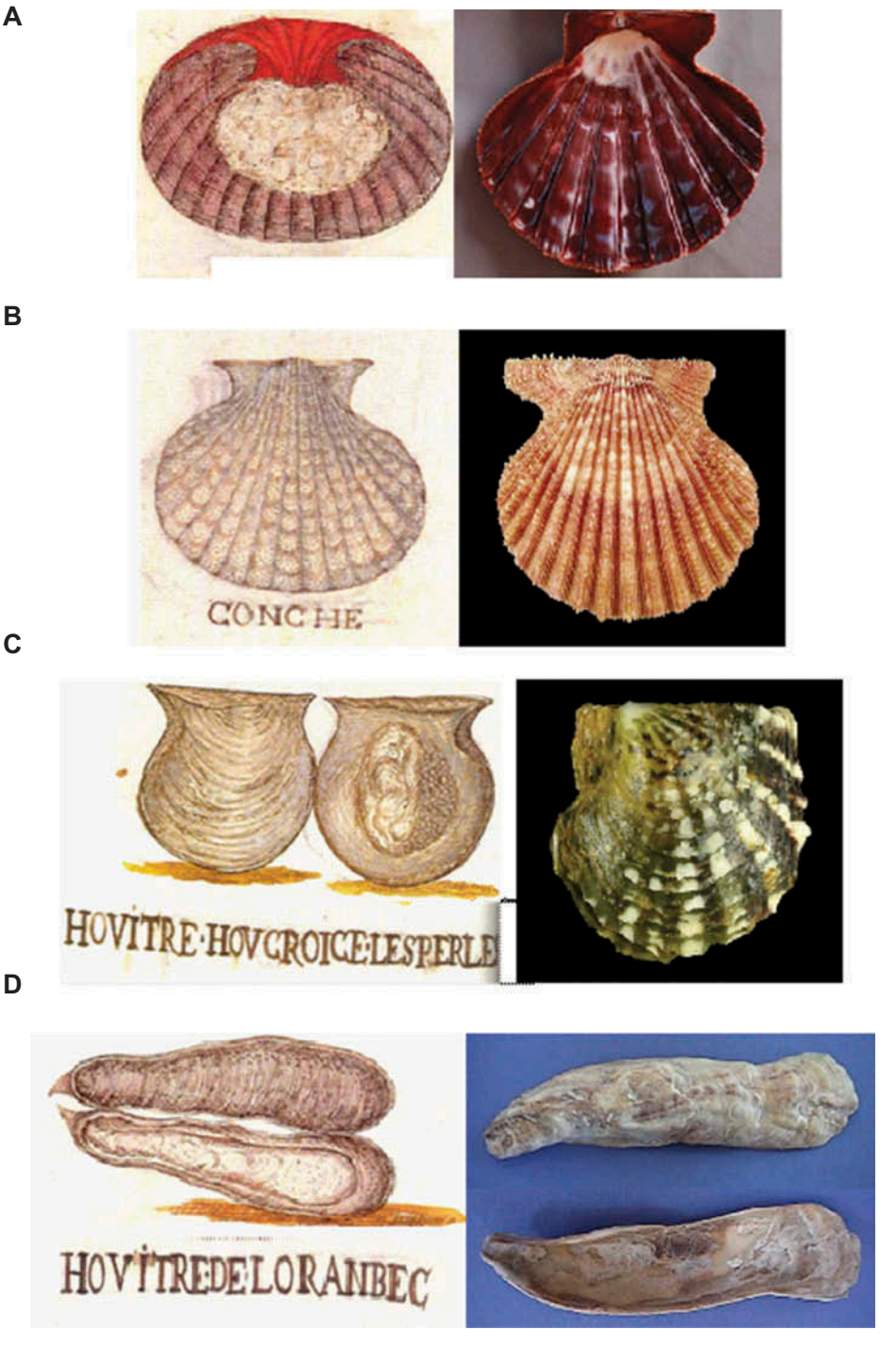

Figure 1. Illustrations of molluscs in *The Drake Manuscript* (left), © The Morgan Library & Museum, New York. Corresponding contemporary images of the species (right) proposed to be the subjects of the anonymous artist's illustrations. Mollusc species include (A) *Nodipecten nodosus* (Linnaeus, 1758) lions-paw scallop, © Caledonian Seashells. Reproduced by permission of Caledonian Seashells (www.caledonianseashells. com).

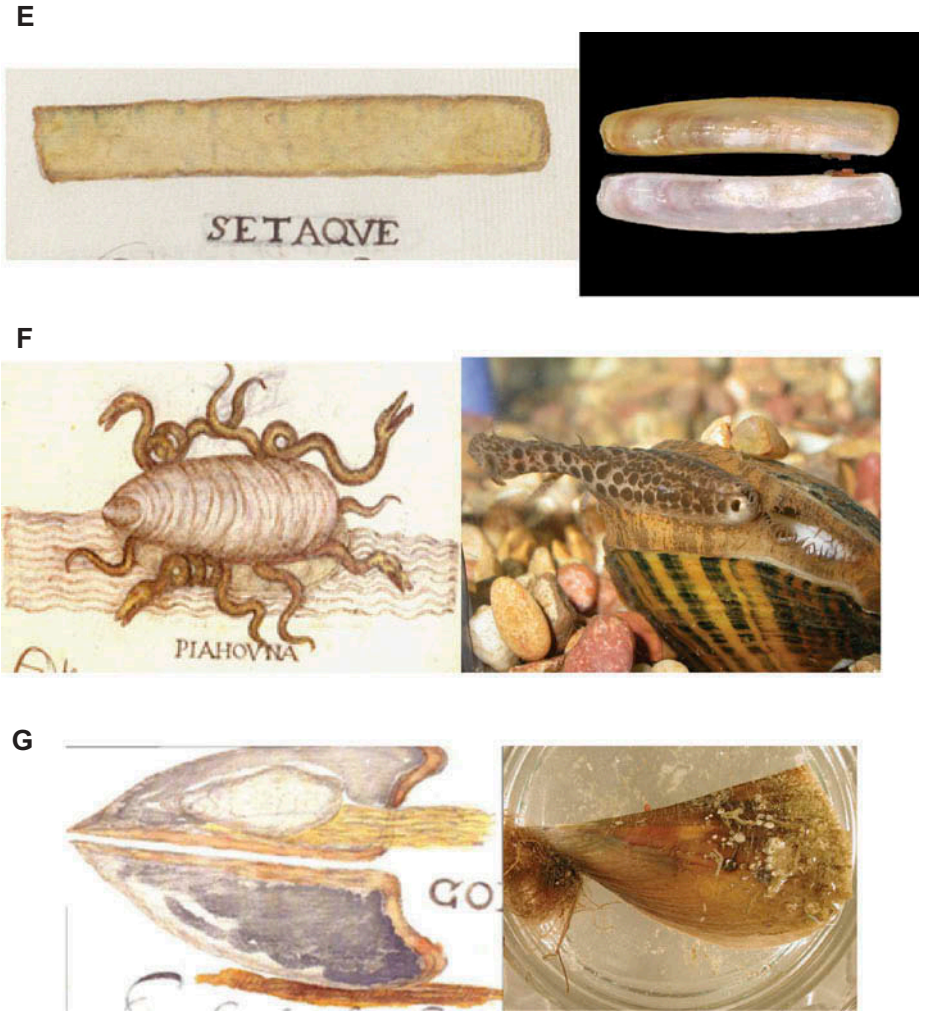

Figure 1. (*Continued*) (B) *Lindapecten muscosus* (Wood, 1828) rough scallop, © Guido and Philippe Poppe. Reproduced by permission of Guido and Philippe Poppe www.conchology. be); (C) *Pinctada imbricate* Röding, 1798 Atlantic pearl-oyster, © Guido and Philippe Poppe. Reproduced by permission of Guido and Philippe Poppe (www.conchology.be); (D) *Crassostrea virginica* (Gmelin, 1791) eastern oyster, © Reuben Goforth. Reproduced by permission of Reuben Goforth; (E) *Solena obliqua* (Spengler, 1794) oblique jackknife, © Association Française de Conchyliologie. Reproduced by permission of Association Française de Conchyliologie (www.xenophora.org); (F) unknown unionid clam with image of Lampsilis reeveiana for comparison, © Chris Barnhart. Reproduced by permission of Chris Barnhart ChrisBarnhart@MissouriState.edu); (G) *Atrina rigida* (Lightfoot, 1786) stiff pen shell, © Jon Fajans. Reproduced by permission of Jon Fajans, Online Resource Guide for Florida Shellfish Aquaculture (http://shellfish.ifas.ufl.edu). Permission to reuse the images must be obtained from the rightsholder.

Table 1. Invertebrate animals illustrated and described in *The Drake Manuscript*.

Invertebrate family (common name)	Folio	Name in manuscript*	Identified binomial (common name)	Translated caption
Pectinidae (scallops)	43 (1 of 2)	Conche	*Nodipecten nodosus* (lions-paw scallop)	This may as well be called a shell and it grows in a bay which is beside the sea which is called Baillahone [on the Guajire Peninsula in Colombia] onto which empty freshwater rivers. The fish which grows inside is very good and dainty; the shell is red in colour on top and violet inside.
	43 (2 of 2)	Conche	*Lindapecten muscosus* (rough scallop)	This shell is beautiful; it is very rough on top. The Indians use it to grind ginger and peanuts, which is a root from which they make flour which serves them instead of bread.
Pteriidae (pearl oysters)	57v	Houitre Hov Croice les Perles	*Pinctada imbricata* (Atlantic pearl-oyster)	Oyster in which the pearls grow
Ostreidae (oysters)	44v (2 of 2)	Hovitre de Loranbec	*Crassostrea virginica* (eastern oyster)	Oyster from Loranbec
Solenidae (razor shells)	44v (1 of 2)	Setaque	*Solena obliqua* (oblique jackknife)	This is a green-coloured stone which is found among the sea beds where they fish for pearls, that is at La Margarita. It give off a sound like glass and is very excellent for all pain of the flanks, being laid on the painful side.
Unionidae (freshwater mussels)	34	Piahouna	Exact species unknown	This is a sort of mussel in which grows a fish – similar to a conger-eel which has the head of a snake. It is found in freshwater streams and is not good eating because it is bitter, reeking of mud – oily and sweetish.

(*Continued*)

Table 1. (Continued).

Invertebrate family (common name)	Folio	Name in manuscript*	Identified binomial (common name)	Translated caption
Pinnidae (pen shells)	47 (2 of 2)	Conche	*Atrina rigida* (stiff pen shell)	It grows where one fishes for pearls. In this conch is found a certain hair like human hair the colour of gold and it is very excellent for people who have an earache or who are somewhat deaf. They dry it in the sun and then put it in their ears and immediately feel its benefit. The negroes often use it, their ears being hurt by frequent dives.
Lobster	49	Hommar	Nephropidae sp.	It is found in the sea at an island called Bastimentos between Nombre de Dios and the River Sagre, being violet in colour and having red claws.
Horseshoe crab	49	Caxquenoc	*Limulus polyphemus*	Crab of Florida

*V and U are given the same letter in Old French.

offset umbo, and the growth rings are usually not strongly defined. Given that the artist often took considerable liberties in portraying characteristics of other subjects, it is readily conceivable that the placement of the umbo and intensity of the annuli are exaggerated in the illustration. The description of this as an 'oyster in which the pearls grow' (Table 1) and the rendering of pearl fishing in illustration f. 57 are also consistent with the ecology of this pearl-bearing oyster species. The weight of evidence therefore suggests that this illustration depicts a specimen of *P. imbricata.*

Illustration f. 44v (2 of 2) (Figure 1D) is described as an 'oyster from Loranbec,' presumably from the Atlantic coast of North America between Florida and Newfoundland (Janick 2012) (Table 1). Oysters in the Family Ostreidae are bivalve molluscs generally characterized as having irregular, unequal valves, the lower of which is cemented to a solid object, that is often another individual or individuals of the same species. Individual morphology is therefore strongly influenced by the surrounding environment. The specimen for *The Drake Manuscript* rendering was most likely *Crassostrea virginica* eastern oyster, which usually exhibits narrow, elongated valves under crowded conditions. The location of collection for the specimen is also consistent with the distribution of *C. virginica*, which extends north to the Gulf of St. Lawrence.

Clams

Illustration f. 44v (1 of 2) (Figure 1E) of *The Drake Manuscript* depicts a bivalve mollusc that is described as a 'green-coloured stone' that 'gives off a sound like glass' (Table 1). It is likely that the artist recovered a single spent valve from *Solena obliqua* oblique jackknife that served as the subject for this illustration. This species is characterized by a shell morphology and shiny green periostracum consistent with the illustration, and an isolated spent valve would appear to be a stone to an amateur naturalist. Further, it is not unusual for the calcium carbonate structure of mollusc shells to emit a tone similar to that resulting from a strike upon glass. There are other razor clam species that could have also served as the specimen obtained by the author, including *Ensis directus* Atlantic jackknife or *S. viridis* green jackknife. However, the location where the specimen was obtained, La Margarita off the coast of Venezuela (Table 1), suggests that the specimen was most likely *S. obliquus* given the more northerly distributions of the other possible razor clam species.

Illustration f. 34 depicts a mollusc described as 'a sort of mussel in which grows a fish – similar to a conger eel' that is 'found in freshwater streams' (Table 1, Figure 1F). Freshwater mussels in the families Unionidae and Magaritiferidae (Order: Unionoida) are common inhabitants of streams and rivers of eastern North America. Given the characterization of the habitat from which the specimen was collected as freshwater, it is probable that it was a unionoid. Bivalves of the order Unionioda have a unique life cycle that includes a parasitic larva (glochidium) that encysts on gill filaments and fin rays of host fishes, where they remain for a period of weeks to months until they metamorphose and drop from the cysts (Cummings and Mayer 1992). Females of some unionoid species, particularly members of the genus *Lampsilis*, exhibit extensions of their mantles that are visually very similar to conspecific fishes (e.g. Figure 1F). These are commonly referred to as 'lures' given their

apparent purpose of simulating prey that attract the attention of predatory fishes. When a predatory fish attempts to feed on the lure, female unionoids with such lures forcefully expel glochidia into the water column, thus increasing the likelihood that the larvae will come into contact with and encyst on its gills and/or fin rays. Another strategy used by some unionoids to enhance transfer of glochidia to fish hosts is the production of conglutinates, or masses of eggs that are typically cylindrical in shape and are sometimes pigmented such that they resemble larval fishes (Obermeyer et al. 2006). It is also possible that the artist was depicting this reproductive strategy in drawing the freshwater mussel with multiple small fish associated with it. Like many of the other illustrations in *The Drake Manuscript*, this illustration is both exaggerated and fanciful, although the description and rendering both have elements to indicate that the specimen was a unionoid mussel species exhibiting a mantle lure or conglutinate. However, there is insufficient taxonomic and locational information to determine the particular unionoid species that served as the specimen.

It is particularly notable that the illustration of the unionoid mussel appears to be the earliest known depiction of the unique mantle lure or conglutinates exhibited by some species in this taxon. Valledor de Lozoya and Arujo (2011) conducted a thorough review of the history of freshwater mussel iconography, and they identified illustrations dating back to the late 15th century. Not surprisingly, many of the early illustrations lacked anatomical details or were based on human activities exploiting freshwater mussels as a prized source for pearls. More detailed illustrations including species names were found from mid-16th-century sources, although these depictions focused on the shells of the animals and not living individuals in natural conditions. The first known illustrations of freshwater mussel anatomy come from late 17th-century sources, and it was not until the 18th century that the first illustration of an individual *in situ* appeared (Valledor de Lozoya and Arujo 2011). Finally, the earliest depiction of a unionoid displaying a mantle lure appears to be an illustration by Isaac Lea in 1838 (Gould 1992), several centuries after *The Drake Manuscript* artist drew what we interpret to be a freshwater mussel exhibiting either a mantle lure or conglutinate. Although the freshwater mussel drawn by the anonymous French artist in *The Drake Manuscript* is clearly exaggerated, the rendering nonetheless reflects a living animal exhibiting a characteristic that is unique to members of this group that had not been previously illustrated.

Pen shell

The bivalve mollusc depicted in f. 47 (2 of 2) is a pen shell of the family Pinnidae, most likely *Atrina rigida* stiff pen shell or *A. seminuda* half-naked pen shell (Figure 1G). The illustration depicts the two inner surfaces of the valves rather than the typical closed orientation that exposes only the spiny exterior surfaces and large byssus. The large open end and overall wedge-shaped structure of the organism in the illustration are consistent with the morphology of these species. Also consistent with the natural history of pinnids is the presence of the large byssus depicted in the illustration as a mass of thread-like structures extending from the valves. The author describes the byssus as ‘a certain hair like human hair the colour of gold’ and indicates that dried byssal threads were used to treat earaches and deafness (Table 1). The use of pinnid byssal threads by humans is not uncommon, and gloves and stockings are made from the byssal threads of Mediterranean species (Abbot and

Morris 1995). There is one substantial discrepancy in the illustration in that the byssus is drawn at the posterior end of the animal, whereas it should be depicted at the anterior end where it serves as an anchor to keep that part of the organism buried. Despite this discrepancy, there is sufficient evidence in both the illustration and the description to suggest that the artist created the rendering based on a specimen of either *A. rigida* or *A. seminuda.*

Lobster

The lobster rendered in illustration f. 49 (1 of 2) (Figure 2A) has several features that depart from those typical of members of the Order Decapoda (Phylum: Arthropoda, Subphylum: Crustacea, Class: Malacostraca). For example, the organism in the rendering has six pairs of appendages (12 total), whereas decapod crustaceans have a maximum of five pairs of appendages (10 total). The rendering also includes mammal-like eyes, a fish-like tail, and an irregular number of antennae (i.e. three) where there should be two pairs. Despite these discrepancies, there are elements of both the rendering and description that suggest that the artist's specimen was *Panulirus argus* Caribbean spiny lobster, one of several species of Caribbean lobsters (Figure 2). One feature of the rendering that firmly contradicts the specimen as *P. argus* is the presence of large chelipeds as the first pair of appendages. *Panulirus argus* lack such chelipeds, although they are prominent features of most large decapods such as *Homarus americanus* American lobster. However, it is possible that the artist mistakenly identified the smaller pair of antennae present in this species as chelipeds given their bifurcated morphology and their often red coloration. This would explain both the additional pair of appendages described above and the presence of chelipeds in the rendering. It is also possible that the artist simply added the large chelae because many lobster species have such features and, as demonstrated above, the artist was prone to some exaggeration and even misrepresentation (e.g. mammal-like eyes on invertebrates) in his renderings. The description of the specimen as violet in colour is consistent with *P. argus* given that many individuals have purplish coloration in life (Table 1). The illustration also depicts multiple large 'horns' in the vicinity of the head (albeit highly exaggerated), and such structures are diagnostic characters of *P. argus*, particularly over the eyes. Another pair of these structures that is oriented from the anterior to posterior of the organism is likely the artist's rendering of the particularly large conical antennae of *P. argus.* Despite the discrepancies in this illustration, the description of the capture location as 'Bastimentos between Nombre de Dios and the River Sagre' (Table 1), which is most certainly Isla Bastimentos off the coast of Panama, makes the identity of the animal depicted in this illustration very likely to be *P. argus*.

Horseshoe crab

There are two renderings of *L. polyphemus* (Figure 3A), one labelled LEDESVS (le dessus = top) and the other LEDESOUS (le dessous = bottom) representing the dorsal and ventral views of *L. polyphemus*. The name 'Caxquenoc' is clearly related to the Algonquian word *Seekanauk* for horseshoe crab (http://www.coastalcarolinaindians.com/updated-algonquian-word-list-by-scott-dawson/). Both views are painted in a reddish-brown colour with the dorsal surface more intensely coloured than the

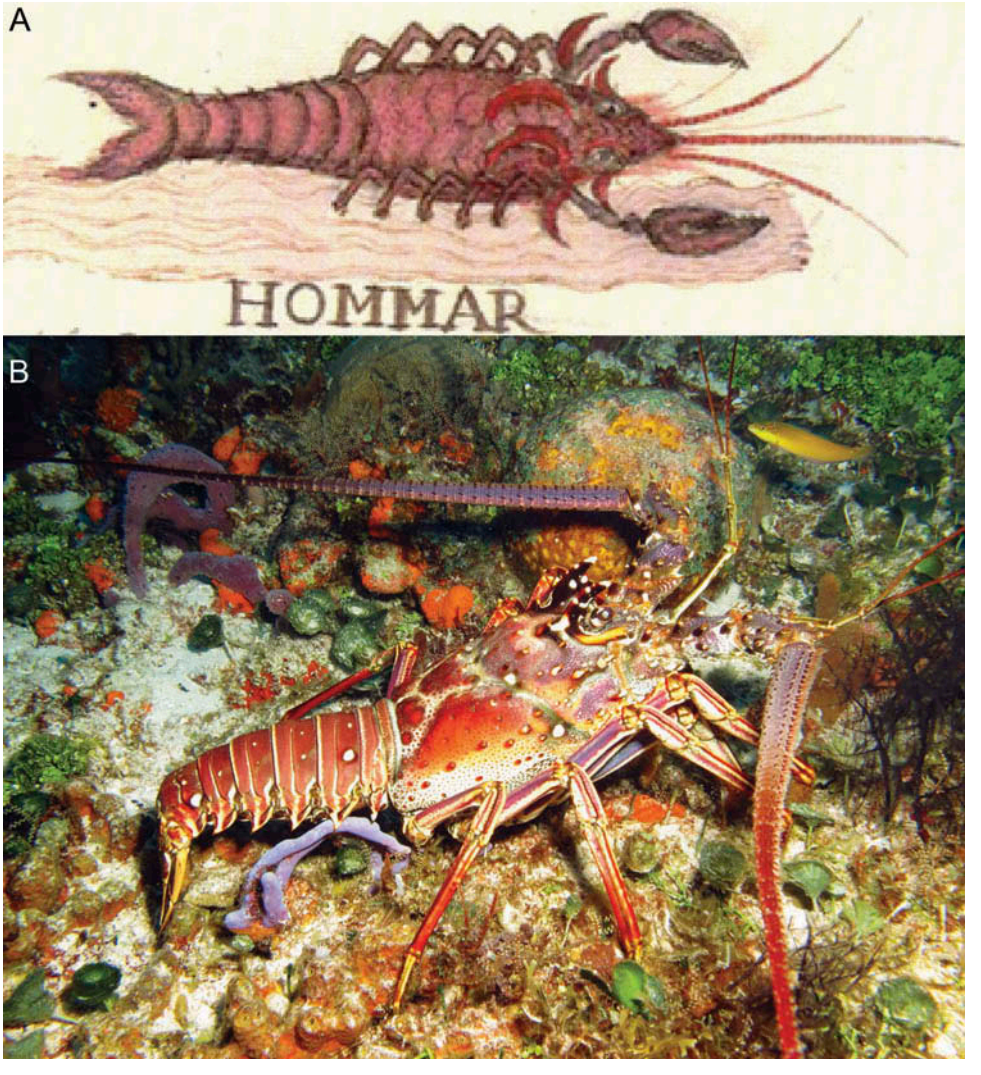

Figure 2. Illustration of (A) a lobster in *The Drake Manuscript*, © The Morgan Library & Museum, New York; (B) corresponding contemporary image of the species proposed to be the subject of the anonymous artist's illustrations. The lobster species is *Panulirus argus* (Latreille 1804) Caribbean spiny lobster. Image of *P. argus* © Florent Charpin. Reproduced by permission of Florent Charpin (www.reefguide.org). Permission to reuse must be obtained from the rightsholder.

ventral surface. Carapace coloration in live horseshoe crabs tends to be monochromatic but can vary substantially in brightness. Much of this variation reflects the influence of the post-moult environment on their carapaces; freshly moulted animals have relatively uniform light green carapaces that become degraded and discoloured by the highly variable environment of the intertidal zone. The carapace in the depiction shows five prominent stripes, or grooves, and no eyes, whereas living horseshoe crabs exhibit three grooves in which two obvious compound eyes are

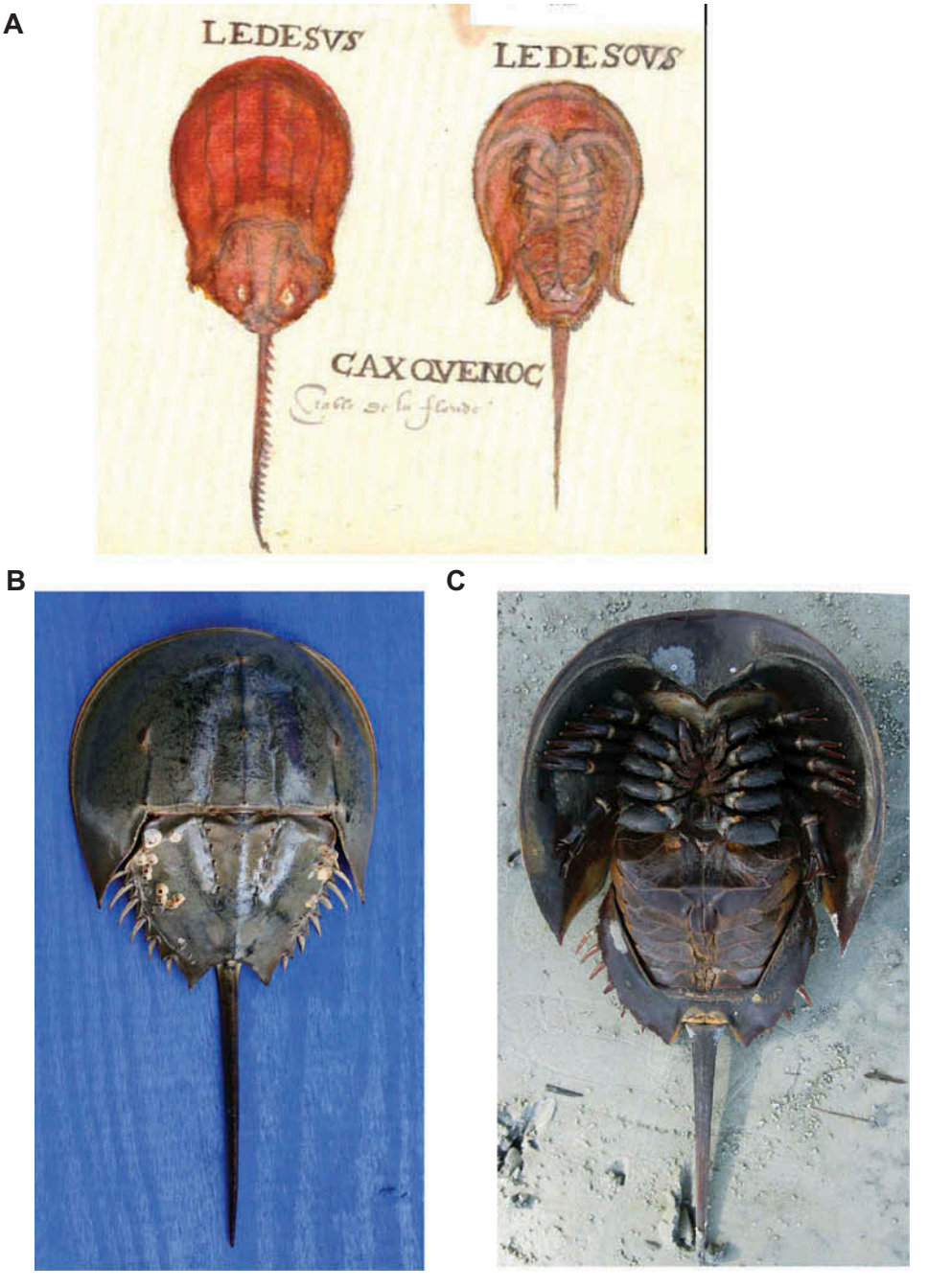

Figure 3. Illustrations of the dorsal and ventral views of a horseshoe crab in *The Drake Manuscript*, © The Morgan Library & Museum, New York. (A); corresponding contemporary images of the dorsal (B) and ventral (C) surfaces of live *Limulus polyphemus* provided for comparison. Dorsal and ventral horseshoe crab © Reuben Goforth. Reproduced by permission of Reuben Goforth. Permission to reuse images must be obtained from the rightsholder.

found in the outer groove and two considerably smaller median eyes, or light receptors, are found above the middle groove (Figure 3).

The dorsal view in the artist's rendering is elliptical with a length–width ratio of 1.47 as compared to the almost round shape (length–width ratio typically 0.85) of most horseshoe crabs. However, there is generally considerable variation in horseshoe crab morphology, including more elongated carapaces. There are also two symmetrical pale markings in the dorsal view of the illustration that are likely the artist's rendering of mating scars on its posterior body segment (opithsosoma). These scars are acquired during mating when an adult male attaches to a female's opithsosoma using modified pedipalps (claspers) and is thereafter dragged around by the female as mating commences. While the female carries the male around, the eggs deposited in shallow pits dug by the females are fertilized by the male and then covered with sand. The site where the males grip the females using the claspers becomes worn on the dorsal surface, yielding the mating scars in the artist's rendering. The light coloration of the mating scars in the illustration indicates that they had recently been created since these markings typically darken with time.

True crabs are crustaceans (subphylum Crustacea) that possess chewing mouthparts (i.e. mandibles) and 10 appendages in five pairs, including two anterior chelipeds. In contrast, *L. polyphemus* is a chelicerate (subphylum Chelicerata) that is more closely related to spiders and other arthropods that lack mandibles. Also in contrast to true crabs, *L. polyphemus* has 12 appendages in six pairs located in the centre of the anterior body segment, or prosoma, that all terminate in claw-like pincers. The most anterior pair of appendages is composed of two chelicerae that are used to carry food to the mouth. However, there are some discrepancies between the artist's illustration and these characteristics. For example, the illustration of the ventral surface in Figure 3 only shows four similar pairs of walking/eating legs between the mouth and the book gills located on the ventral surface of the opisthosoma. Additionally, while one pair of small chelicerae is included in the rendering, it is somewhat obscure. On the other hand, the fact that all of the large legs are similar indicates that this is a female *L. polyphemus*, and this is consistent with the depiction of mating scars in the dorsal view provided in the illustration. A male, by contrast, would have its most anterior walking legs terminating in thick hook-like claspers used to hold onto the carapace of a female during mating as described above.

The artist provides a clear rendering of the gill book that makes it possible for these animals to come onto land and breathe air for long periods of time. The animal has muscular control over these structures and can wave its gill leaves back and forth. Both views of the animal show the tail spine (telson). Here the artist has taken some license by rendering the dorsal view of the tail with many sharp prongs projecting laterally when in fact they actually project dorsally; the tail cannot rotate. The ventral view accurately shows no trace of these prongs. It is clear that the unknown artist altered the direction of the projections in the dorsal view in order to better define them. These spines are noticeable on both the dorsal and ventral view of live specimens, although it is important to note that these spines usually become worn down in mature individuals, rendering the telson smooth. The mating scars in the illustration indicate that the individual was not newly moulted, so the spines depicted were almost certainly exaggerated, or the drawing may be a composite of multiple individuals.

Source of the illustrations

The paintings of the bivalve molluscs appear to be made by someone with first-hand knowledge of the animals and who used them as subjects for sketches in a notebook. Although some of the paintings are quite crude and even whimsical in the case of the freshwater 'mussel', they clearly are based on direct observation. For example, the mussel image shows snake-like creatures emerging from the shell (Figure 1F), which can be explained by the mantle extensions used in some unionid species as lures. The illustration of the lobster has some gross inaccuracies related to the large chelipids. In contrast, the two views of the horseshoe crab are quite accurate in comparison with some of the organisms less reliably portrayed. Finally, the artist often made mention of how the illustrated animals tasted, further demonstrating direct experience with these organisms. The bivalve molluscs illustrated in *The Drake Manuscript* are therefore likely to be based on the encounter with these organisms in the Americas by the anonymous French author.

While it appears that the rendering of *L. polyphemus* in *The Drake Manuscript* (Figure 3) was made directly from nature, another interpretation is possible. In 1585, a skilled artist named John White produced images of plants and fish in Roanoke and Puerto Rico. A number of White's illustrations, including a tortoise, flying fish, mamey, plantain, and pineapple (Janick 2012), are also found in *The Drake Manuscript*. Furthermore, White's drawings were incorporated in a number of contemporary works. For example, three images (dolphin fish, triggerfish, and iguana) appear in the maps of Baptista Bozio, and one image of milkweed appears in Gerard's 1597 herbal (Sloan 2007; Janick 2012; Janick and Phippon 2013). It is possible that the illustration of *L. polyphemus* in *The Drake Manuscript* was based on a lost drawing of John White. There is evidence that White and Boazio accompanied Sir Francis Drake on his return voyage from Roanoke to England in 1585 after the rescue of the ill-fated colonists, and Janick (2012) conjectured that the anonymous artist of *The Drake Manuscript* was on the same voyage, based on evidence from logs in Drake's 1585–1586 voyage to the West Indies that Frenchmen were picked up in Cartegena. Although the illustration of *L. polyphemus* in *The Drake Manuscript* indicates it is from Florida, John White may have visited the coast of Florida in 1584 in the preliminary voyage of Philip Amadas and Arthur Barlow to Roanoke (Sloan 2007, p. 28) and also visited Florida in 1590.

John White did include *L. polyphemus* images in a watercolour entitled *Indians Fishing* (Quinn 1985, p. 190, 191; Sloan 2007, p. 109), thought to have been made in Roanoke in 1585, and this appears to be the first image of horseshoe crab in the New World although there are earlier images from Asia (Sekiguchi 1988). The White watercolour (Figure 4A) shows a complete and a partial image of swimming *L. polyphemus* in the lower right of the image, drawn in a very sketchy manner. The carapace is grey, with a length–width ratio of 1.31, and a telson about three-quarters the length of the carapace, with three pairs of legs extending from the carapace of which the anterior pair appears to end in a pincer. Two lateral eyes are also apparent on the carapace.

The illustration of *L. polyphemus* is further elaborated in the modified drawing of *Indians Fishing* in the report of the Roanoke colony by Thomas Hariot reprinted by Theodore De Bry in 1590 with etchings (Figure 4B) derived from White's paintings (Hariot 1590; Sloan 2007, p. 108). This etching contains two complete images of *L.*

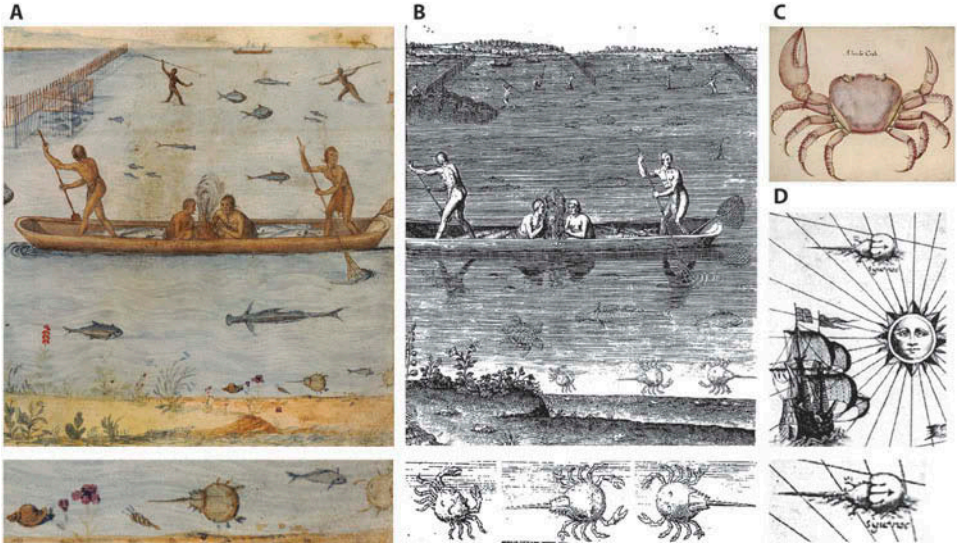

Figure 4. Illustrations of horseshoe crab (*Limulus polyphemus*) and land crab (*Cardisoma guanhumi*) taken from: (A) painting ca. 1585 by John White entitled 'Indians Fishing' showing horseshoe crab in the lower right, © Trustees of the British Museum. Reproduced by permission of The British Museum; (B) engraving of Theodore De Bry of 1590 after White showing horseshoe crab and land crab, reproduced by permission of The Huntington Library, San Marino, California; (C) land crab in a painting by John White, © Trustees of the British Museum. Reproduced by permission of The British Museum; (D) engraving of horseshoe crab in a 1613 map of New France drawn by David Pelletier from sketches of Samuel de Champlain labelled *siguenoc* © V. Dickinson. Reproduced by permission of V. Dickinson. Permission to reuse images be obtained from the rightsholder.

polyphemus, including an image of a land crab not found in the watercolour (Figure 4B).

The de Bry etchings of *L. polyphemus* show more detail than the watercolour image of White. The elliptical shape has a length–width ratio of 1.25 and it shows five pairs of appendages extended from the carapace, with four pairs ending in pincers and the posterior appendage terminating in a clubbed shape. The chelicerae are correctly not shown in this lateral view, although the anterior pincer is exaggeratedly large. The image also correctly shows two lateral compound eyes. It is clear that the de Bry image is an elaborated version of the images in White's painting. However, it must have been based on a clearer image as it is unlikely that De Bry could have made up the details of the appendages. Given the sketchy nature of the White watercolour image, it is likely that it was derived from a detailed drawing or painting that has been lost. We believe this archetypic image of *L. polyphemus* must have been as detailed as a land crab image of White (Figure 4C).

The White watercolour can be dated to 1585, and the sketchy image may very well be the earliest surviving image of *L. polyphemus* (Quinn 1985, p. 190, 191; Dickenson 1998, p. 62, 63). An image of horseshoe crab labelled *siguenoc* (Figure 4D), most certainly an alternate form of *caxquenoc* found in *The Drake*

Manuscript, can be found in a 1613 map of Canada (Dickenson 1998) that is very similar to the paintings of White. Three other horseshoe crab species dwell along the shores of other continental coasts, including the east coast of India, the east coast of Indochina, and the east coast of Japan. Because highly developed civilizations with rich artistic traditions existed in those locations for thousands of years prior to the creation of the renderings discussed here, we cannot rule out the possibility that earlier representations of horseshoe crabs may have been created by these cultures before the late 16th century. What we can say is that John White's 1585 watercolour and *The Drake Manuscript* clearly display representations of *L. polyphemus* as well as other aquatic invertebrates in the late 16th century.

It seems clear that the paintings of aquatic invertebrates in *The Drake Manuscript*, while crude, are nonetheless quite naturalistic, and we conclude that they are primarily based on first-hand observation, especially given the mention of 'taste' in reference to many of the rendered taxa. It is likely that the paintings by the anonymous artist were made from early sketches. However, we also suggest that the painting of *L. polyphemus* may have been at least influenced by a lost drawing of John White versus being based solely on personal observation.

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