The first records of deep-sea fauna – a correction and discussion

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Abstract

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1 Introduction

When books or review-papers give in their introductory section a short overview of the history of deep-sea research, the recovery of a basket star by Sir John Ross in 1818 from deep-waters of the North-West passage is often cited as the first organism that was brought up from the deep-sea (Menzies et al. 1973; Tyler 1980; Gage & Tyler 1991; Ramirez-Llodra et al. 2010). This is not correct. The first published record is considerably older: the upper bathyal stalked crinoid *Cenocrinus asterius* (LINNÉ) was brought up, probably on fishing lines on several occasions, in the Caribbean (Thomson 1873), and two specimens reached Europe and were already described in 1761 and 1762, respectively. In addition, several descriptions of deep-sea fishes appeared in the late 18th and early 19th century, again predating Ross' finding of the basket star.

To put these historical finds in context, we want to give in the following paragraphs an overview of

- deep soundings and dredgings up to the times of the Challenger expedition;

- the historical records of basket stars and stalked crinoids;
- possible explanations why the Ross expedition became uncritically cemented in the deep-sea literature whereas the earlier finds of *Cenocrinus asterius* and other captures of deep-sea creatures were neglected.

For practical reasons all the depths given in the historical literature are converted to meters.

2 Sounding and sampling the deep sea

Sounding ~~the~~ water depths with line and plummet had been in use since the first ships went to the oceans yet it had always been the shallow waters near the land that were in the focus of the navigators. Those soundings were used for the first time in nautical maps in the 16th century, and isobathic coastal maps were introduced in 1737 (Murray 1895; Murray & Hjort 1912).

We here follow Gage and Tyler (1991), Herring (2002), Tyler (2003), Thistle (2003), Snelgrove and Grassle (2008) and others and let the deep-sea start below 200 m. The first scientific attempt at sounding the deep-sea is ascribed to Magellan who tried in 1521 unsuccessfully to reach the bottom between two pacific coral islands with a line measuring between 180 and 360 m (Murray 1895; Murray & Hjort 1912). The conclusion that the expedition had here arrived at the deepest part of the ocean appears rather naïve (Murray 1895).

The next sounding that found its way into the deep-sea literature was in an apparent depth of 1250 m, recorded in 1773 east of Iceland by Captain Constantine Phipps aboard the HMS Racehorse (Rice 1975) but this depth must be read with caution (see below). The soundings undertaken in 1818 during the John Ross expedition searching for the Northwest passage in the Arctic (Ross 1819) with alleged depths of up to 1950 m in ~~the~~ Baffin Bay appeared like a quantum leap. Furthermore, for the first time an animal was brought up from a depth that seemed to be accurately recorded. But of course there are major problems with this expedition. The captain’s diary, the shipboard recordings, and the subsequent publications were inaccurate and sometimes contradictory (Rice 1975). The actual depths of the deepest soundings were only around half of the published values and did certainly not exceed 1100 m (Rice 1975). The famous basket star that was allegedly caught entangled in the sounding line 370 m above the weight (!) must also have come from a depth of around 1000 m. This is still impressive, and had this result been more widely disseminated, it had perhaps prevented the uncritical prevalence of Forbes' theory of an azoic zone below 550—600 m (Forbes 1844; Rice 1975; Anderson and Rice 2006).

Similar problems with a large divergence between apparent and true depth certainly apply to all the deep soundings of the early 19th century. The James Clark Ross expedition for example allegedly sounded in the Atlantic east of Brazil with a line in excess of 8400 m without reaching the bottom (Ross 1847; Murray 1895). Yet such depths are nowhere to be found in this region!

The scientific sampling of the deep-sea received a veritable boost when dredging the seabed became possible at ever greater depths. The brilliant naturalist Edward Forbes was a pioneer in that field. By 1839 he had already dredged at various places around the northern British Isles (Anderson and Rice 2006) and had developed a zonation of life from the littoral down to mid-shelf depths. In 1840 Forbes joined a campaign on the HMS Beacon to conduct surveys in the eastern Mediterranean. It was his work on the bathymetric distribution of life in the ~~Aegaeis~~, based on more than 100 dredgings ~~down~~ to a depth of 240 m (Murray 1895)~~,~~ that proved most influential. Forbes noted that life became ever sparser with increasing depth and concluded by interpolation that life would vanish below a depth of about 550 m (Forbes 1844).

Such a theory of the azoic deep-sea had already been developed e.g. by the French naturalist François Péron who thought that the bottom of the deep-sea was covered with eternal ice (!) and therefore without life (Murray 1895). Likewise, the British geologist Henry de la Beche had postulated a lifeless deep-sea on theoretical grounds (Anderson and Rice 2006) but it ~~were~~ the detailed investigations of Forbes that ensured a staying power for the theory of azoic deep-sea bottoms. In those days it seemed only logical that the dark, ice-cold environment without primary production where huge pressures acted would be hostile to life (Anderson and Rice 2006).

Of course there were already in 1840 strong indications that life was present in the deep-sea below 550 m. The John Ross Arctic expedition had in 1818 recovered life from much greater depths. Dredgings made between 1839 and 1843 during the Antarctic expedition of James Clark Ross had brought up samples full of life from depths up to 730 m (Murray 1895; but again these depths must be read with caution).

Especially influential was the work of the Norwegian naturalist Michael Sars who published in 1850 a list of animals that were dredged from depths of more than 550 m off the coast of northern Norway (Murray 1895). Later work was done together with his son Georg Ossian

Sars, and they published their new finds from deep waters, including the stalked crinoid *Rhizocrinus lofotensis* (SARS, 1868). This new species was the first stalked crinoid to be brought up from a defined depth. It spurred considerable interest among fellow marine researchers, mainly Thomson and Carpenter, and had a large impact on the future direction of deep-sea research (see below).

When a telegraph cable between Britain and America was ~~in the planning,~~ further evidence for life at great depths ~~were~~ found. In 1860, Georg Charles Wallich aboard the HMS Bulldog sounded and sampled the seabed in the northern Atlantic. In one sounding to a depth of 2300 m, he found several brittle stars entangled around the rope (Wallich 1862). For Wallich this proved that life existed at great depths and was by far the most important sounding ever (and at the same time he dismissed similar results obtained by others; see Rice et al. 1976; Rozwadowski 2005). Yet his results and conclusions were not widely accepted which later led him to engage in a bitter feud with Thomson and Carpenter (Rice et al. 1976).

Conclusive proof for the existence of life on very deep bottoms came when a telegraph cable laid in 1857 between Sardinia and the north African coast failed in 1860. The 70 kilometers brought up for repair came from a depth of more than 2000 m, and together with the cable many animals from the seabed were recovered. Most notable were some specimens that were attached to the cable itself, especially a coral of the genus *Caryophyllia* that had its base moulded on the structure of the cable (Murray 1895).

Further indications for rich life at great depths came from various sources, e.g. the dredgings from Torrell's expedition to Spitsbergen in 1864, ~~or~~ the recovery of the glass sponge *Hyalonema* by fishermen, first in Japan, then in 1868 ~~also~~ from the deep-sea off Portugal (Murray 1895). In the following years sporadic successful dredgings from deep environments were obtained, but systematic investigations of the deep-sea floor really only commenced with the British expeditions aboard the HMS Lightning in 1868 and the HMS Porcupine in 1869/1870. The objective of these expeditions was to investigate the distribution of life on the deep-sea floors, to look for "living fossils" and to document the temperatures of Atlantic waters (Mills 1983; Rozwadowski 2005). Especially the Porcupine cruise was highly successful, with many dredgings full of life ~~down~~ to a depth of more than 3500 m (Murray 1895; Mills 1983; Rozwadowski 2005). It was also during these expeditions that new dredges, sounding devices and other equipment were tested for their application in deep-sea research (Mills 1983; Rozwadowski 2005). The results of these expeditions were also instrumental for the writing of what could be called the first textbook on deep-sea biology (Thomson 1873).

Finally, during the subsequent circumnavigation of the HMS Challenger (1872-1876) it could be proven once and for all times that life existed in all oceans and at all depths.

3 The neglected part of deep-sea sampling

Yet sampling of deep-sea animals was not restricted to scientific campaigns that sounded and dredged the bottoms. This environment was also sampled by fishermen who put their lines and hooks down to considerable depths and retrieved many unanticipated species in addition to their planned catches. It was such findings that provided the earliest records of deep-sea life. These were stalked crinoids from the Caribbean (see below) and various deep-sea fishes from the Azores, Madeira, northern Spain, Sicily, and Antillean islands (e.g. Günther 1887).

These fishes include the oarfish *Regalecus glesne* Ascanius, 1772, the hatchetfish *Sternoptyx diaphana* Hermann, 1781, the ribbonfish *Trachipterus trachypterus* (Gmelin, 1789), the tube-eye *Stylephorus chordatus* Shaw, 1791, the viperfish *Chauliodus sloani* Bloch & Schneider, 1801, the scaly dragonfish *Stomias boa* Risso, 1810, and the grenadier *Coelorinchus caelorhincus* Risso, 1810. Most of these had been caught floating near the surface and sometimes in coastal environments (Günther 1887) but they nevertheless are true deep-sea species!

Because the echinoderm groups of the basket stars and the stalked crinoids played a crucial role in the history of deep-sea research, both these groups are treated in more detail below.

4 The historical record of basket stars

Most basket stars live on hard bottoms, often clinging to corals or sponges, in deeper shelf and upper bathyal environments (Lyman 1882; Koehler 1909; Clark 1915; Hendler 1996) but some also occur in water depths as shallow as 10 m as well as in abyssal depths (e.g. Clark 1915; Emson et al. 1991; Hendler 1996). Up to the times of the first deep-sea expeditions every finding/recovery of these animals was a lucky incidence that, not least because of their strange appearance, received considerable attention. Their unusual morphology is reflected in their naming: “Caput medusae”, “Gorgonocephalus”, head of the medusa. They are among the largest ophiuroids and are voracious predators that feed on megaplankton (Emson et al. 1991; Rosenberg et al. 2005).

The oldest valid name is *Gorgonocephalus caputmedusae* (LINNÉ, 1758) but different basket stars were already recorded earlier. Rondelet described and nicely illustrated the Mediterranean species (Rondelet 1555, p. 121) which was later copied by Gessner (1558) and Aldrovandi (1602). In 1675, a northern European species was described for the first time (Martens 1675; he gives a strange description p. 88: “The other starfish, body decagonal, below (mouth) six-rayed star”; our translation), which might indicate that this specimen was hexamerous. This was followed in 1705 by a Indo-Pacific basket star (Rumph 1705). Linck (1733) was probably the first to recognize several distinct species but his names predate the 10th edition of Linné’s Systema Naturae and are hence not valid.

Linné (1758) based his name ~~obviously~~ on a specimen from Norway that he had described earlier (Linné 1754). It is not evident why he did not mention the description of Rondelet (or Gessner) as he usually did so but the various forms recognized by Linck (1733) were for Linné all the same. Today, of course these are indeed recognized as different species: Rondelet’s Mediterranean species is *Astrospartus mediterraneus* (RISSO, 1826) and the one described by Martens from “Weyhegatt” (probably Weygate Straits, Svalbard) appears to be *Gorgonocephalus arcticus* LEACH, 1819 although six jaws are otherwise not known in that species (S. Stöhr, personal communication 19.08.2014).

Rumph’s species cannot be determined as the figures do not show any key characters. However, ~~it~~ can be excluded ~~that it is *Gorgonocephalus caputmedusae*~~ (S. Stöhr, personal communication 19.08.2014). Unfortunately, that name is routinely used when Rumph’s specimen is discussed in the literature (e.g. Reich (2010) in his essay on the “Swabian Caput Medusae”, which is the crinoid *Seirocrinus subangularis* (MILLER, 1821) from the lower Jurassic Posidonia Shale). When describing natural wonders of the island Cuba, Parra (1787) mentioned and figured two “Estrella ramosa” that were the first published basket stars from the Caribbean. The figures are not very accurate but the specimens probably belong to *Astrophyton muricatum* (LAMARCK, 1816) which has a rather wide distribution in the Caribbean (~~S. Stöhr, personal communication 19.08.2014~~).

The specimen that Ross recovered in Baffin Bay was ~~a~~ *Gorgonocephalus arcticus* LEACH, 1819, and not ~~an~~ *Astrophyton linckii* (LYMAN, 1882) (= *Gorgonocephalus caputmedusae*) as ~~was~~ frequently indicated (Menzies et al. 1973; Tyler 1980; Ramirez-Llodra et al. 2010; see Leach 1819). Ross’ specimen is perhaps still in the possession of the Natural History Museum in London (Rice 1975; Anderson and Rice 2006). This species (Fig. 1) also occurs in the eastern arctic Atlantic, e.g. around Svalbard and off Norway (Koehler 1909), and in the Kola fjord in the region of Murmansk (Fedotov 1926). Like *Gorgonocephalus caputmedusae*, *G. arcticus* (*Astrophyton agassizi* STIMPSON, 1854 is a junior synonym according to Stöhr 2014) is encountered from infralittoral ~~down~~ to deeper bathyal environments (Grieg 1900; Fedotov 1926) but mostly between 15 and 100 m (Fedotov 1926). It is therefore, strictly speaking, not a deep-sea species.

5 The historical record of stalked crinoids and the notion of "living fossils"

The finds of stalked crinoids from deep waters of the Caribbean around 1750 must be considered the first records of deep-sea animals that were published. Yet they were not recognized as that because there were no sounding records tied to those catches, but today we know that they are bathyal species and therefore true deep-sea forms. Already then, however, it was obvious that these finds somehow related to fossils from the distant past, and the concept of "living fossils" was developed almost 100 years before Darwin (1859) introduced this term when discussing the platypus and the South American lungfish (Rudwick 2005).

Much later another species was recovered from a known depth in bathyal environment off northern Norway and immediately caught the attention of the scientific community. It was recognized both as a deep-sea animal occurring well below the depth limit for life according to Forbes and his disciples, as well as a living fossil (see section on *Conocrinus lofotensis*). This proved to have a major impetus for the succeeding planning of deep-sea explorations.

5.1 The "sea palm" *Cenocrinus asterius*

Guettard (1761) described the first known stalked crinoid in detail as "Palmier marin" (Fig. 2). Linné (1767) later named it *Isis asteria* and Lamarck (1816) *Encrinus caput medusa*. It is an isocrinid and now known as *Cenocrinus asterius* (LINNÉ). The remains of the animal were kept as "palmier marin" in the cabinet (collection) of a M. de Boisjourdain at Martinique who obtained it from an officer of a vessel making port there. Unfortunately, the exact location of the catch, presumably by a fisherman, is unknown. However, this crinoid is common in the Caribbean at 200–300 m. It was in fact Madame Boisjourdain who made the link between the living animal and the fossil remains of isocrinids with their pentagonal column and star-shaped columnal facets. Guettard thus presented this animal as a survivor of a disappeared marine world whose *pierres étoilées* (encrinites, entroques, trochites) were topics of doubts as to their nature. Guettard seemed to have been happy to be able to resolve these doubts. He even went on to count the total number of ossicles of the crinoid and arrived at the astonishing figure of at least 128’675! This was even more than Rumph (1705) had counted for his “Caput medusae” with 81’840 ossicles. Guettard also mentioned a superficially similar animal that was caught by whale-fishers in deep waters off Greenland and described by Mylius (1753). Yet this was certainly no crinoid (Guettard 1761) but rather an umbellulid pennatulacean (see Ellis 1755; see also Walch 1769).

Shortly thereafter a second specimen was brought to the attention of the public. It was found near Barbados and described by Ellis (1762). With only the lower part of the crown preserved it was less complete than Guettard’s specimen (Fig. 3). This crinoid has survived ~~up to the present day~~ and is now in the Natural History collections of the Glasgow museums (Rudwick 2005). Ellis also compared his “Encrinus” to British fossils from the Lower Jurassic. In the meantime, *Cenocrinus asterius* has become one of the most studied living stalked crinoids, including numerous in situ observations (Baumiller et al. 1991).

5.2 Crinoid finds between 1762 and 1864

In the years after the publications of Guettard (1761) and Ellis (1762), new stalked crinoid species were sporadically recovered. They were all accidental catches from the Caribbean with no defined depth attached to them. They were largely neglected by marine biologists and had no impact on deep-sea research in the following decades.

In his description of natural objects of Cuba, Parra (1787) gave a figure and a description of another isocrinid and called it “palma animal”. He also undertook the sport~~s~~ of counting the ossicles of this crinoid and arrived at 62’660 without counting the stalk and the cirri. His figure was later reproduced by Gervais (1835) who erected the new species *Encrinus parrae*. This species is today recognized as *Endoxocrinus (Endoxocrinus) parrae* (Gervais in Guérin, 1835) ~~and is locally very abundant in the Caribbean, chiefly at depths between 500 and 600 m~~ (David et al. 2006).

Shortly thereafter another crinoid was described from deep waters of the Caribbean. It was the peculiar *Holopus rangii* d’Orbigny, 1837 which ~~is~~ cement~~ed~~ to the substrate (Orbigny 1837; Grimmer and Holland 1990). This species ~~was~~ observed on hard bottoms, preferentially under overhangs, in depths between 100 and 654 m but its main distribution is upper bathyal (Améziane et al. 1999; Donovan and Pawson 2008). A further species, *Pentacrinus muelleri*, was erected by Oersted in 1856 and later described in more detail by Lütken (1864).

However, *P. muelleri* is considered today a junior synonym of *Endoxocrinus parrae* (David et al. 2006). Finally, *Pentacrinus decorus* was described by Thomson in 1864 (see Carpenter 1884). This species which is now known as *Neocrinus decorus* (THOMSON, 1864) has a wide distribution ~~around Florida, in the Gulf of Mexico and in the Caribbean proper~~ and occurs between ~~150 and 1200 m (Pawson et al. 2009)~~. It is semi-sessile and is capable of rapididly crawling along the bottom with the aid of its arms (Baumiller and Messing 2007).

5.3 *Conocrinus lofotensis*

In 1864 Sars mentioned the find of a new stalked crinoid named *Rhizocrinus lofotensis* (Fig. 4). It was dredged from a depth of about 550 m off the Lofoten Islands and belongs to the bourgueticrinids, a type known at the time only from fossils. The species, now named *Conocrinus lofotensis* (SARS, 1868), was described in detail by M. Sars in 1868 who contended that the deep-sea floor was a refuge for living fossils. The find caused extreme interest in the scientific world that such a living fossil, a sort of degraded Apiocrinite (Carpenter 1884, p. 246), was still to be found in recent seas. This first living example of a stalked crinoid recovered from known depth was one of the reasons that Thomson and Carpenter, both interested in these animals, persuaded the British Admiralty to use the warships HMS Lightning and HMS Porcupine for deep-sea dredging operations (Thomson 1873).

6 Why the early records vanished from the textbooks

The John Ross expedition with its groundbreaking soundings to an alleged depth of more than 1950 m and the recovery of a basket star from such a depth was initially neglected and not cited in the pertinent literature of the early 19th century (Rice 1975). It was only “rediscovered” after opponents of the azoic theory of Forbes were assembling the facts that would prove that animal life existed on deep-sea floors. Afterwards however and well into the 21st century, the John Ross episode became uncritically cemented in the deep-sea literature.

When in 1761/62 the first modern stalked crinoids were reported from the Caribbean, they came from an unknown depth and the scientific interest centered more on their Mesozoic appearance and their role as “living fossils” (e.g. Walch 1769). The deep-sea fishes that were described between 1770 and 1810 likewise came from unknown depths or even surface waters. Only later did we learn that these were bathyal species. Risso (1810) was the first to develop a bathymetric distribution scheme for fishes but this was not tied to actual soundings and open to criticism. The reasons why deep-sea organisms were not recognized as such in the 19th century were thus manyfold:

- Deep-sea organisms brought up by fishing or sounding lines were considered for a long time less reliable than dredgings. It was suspected that organisms might have become entangled higher up in the water column. This also applied to organisms like stalked crinoids or basket stars that are now known to be strictly benthic (Rice 1975).
- For demersal deep-sea fishes, a bathymetric zonation was developed only after the Challenger expedition (Günther 1887). This took even considerably longer for bathypelagic fishes. Some researchers maintained that there was in the open ocean a zone devoid of life between the surface waters and the deep-sea bottom (Agassiz 1888) while others believed in the existence of an intermediate fauna. This was only settled in favor of the second opinion after the German Valdivia expedition (Chun 1900).
- In his masterly treatment of the history of deep-sea research, Murray (1895) gathered all the results of deep-sea explorations that pointed to rich life on deep-sea floors, as had Thomson (1873) done before with lesser depth. It was these texts that hailed John Ross' expedition as an early record-breaking cruise and took the published results at face value. At the same time Murray omitted (in contrast to Thomson 1873) the occurrences of the deep-water stalked crinoids from the Caribbean, although they were of course treated in the Challenger report on the stalked crinoids (Carpenter 1884). Murray's chapter was highly influential and inspired many subsequent historical summaries either directly or indirectly. It should therefore come as no surprise that the early finds of Caribbean crinoids ~~was~~ omitted in most historical introductions (e.g. Murray and Hjort 1912; Menzies et al. 1973; Gage and Tyler 1991; Ramirez-Llodra et al. 2010), a rare exception being Mills (1983). Murray also confounded *Gorgonocephalus arcticus* with *G. caputmedusae* (= *G. linckii*), and the latter name persisted in many of the above mentioned texts.
- While in the times of Forbes the deep-sea started at around the shelf break, during the 20th century the deep-sea was equated by many with deeper bathyal depths or the abyss, i.e. water-depths of more than 500 or 1000 m (e.g. Canganella and Kato 2007). This was perhaps an additional reason that the historical finds of bathyal animals were neglected.

7 Conclusions

The published record of deep-sea organisms goes back to the middle of the 18th century. Stalked crinoids from the Caribbean were the first among these early records. Originally they were not perceived as deep-sea animals yet were instrumental in developing the concept of "living fossils". Consequently, these finds were discussed in the paleontologic literature but largely omitted in the field of marine biology.

When the systematic exploration of the deep-sea commenced during the early 19th century, only dredgings from a "known" depth (even if that depth-sounding was grossly in error) were accepted by the scientific community as reliable indicators of deep-sea life. Apart from 1860, epizoans on telegraph cables that were brought up for repair also became accepted as proof of life in the deep-sea. The catch of a basket star at great depths during the John Ross expedition only became scientific commonplace when Thomson, Carpenter and others started to assemble the facts that would disprove Forbes' theory of the azoic deep-sea.

Accidental catches that would emerge as important evidence of deep-sea life such as those of stalked crinoids from the Caribbean persistently remained neglected through much of the 20th century. This has much to do with the lasting influence of Murray's remarkable chapter on the history of oceanography and deep-sea research in the Challenger report summary (Murray 1895) from which some errors and omissions were perpetuated in the newer literature. It is therefore important that the historical literature is carefully read, evaluated and compared with the original sources, and summary treatments from the 20th and 21st century should not be uncritically followed.

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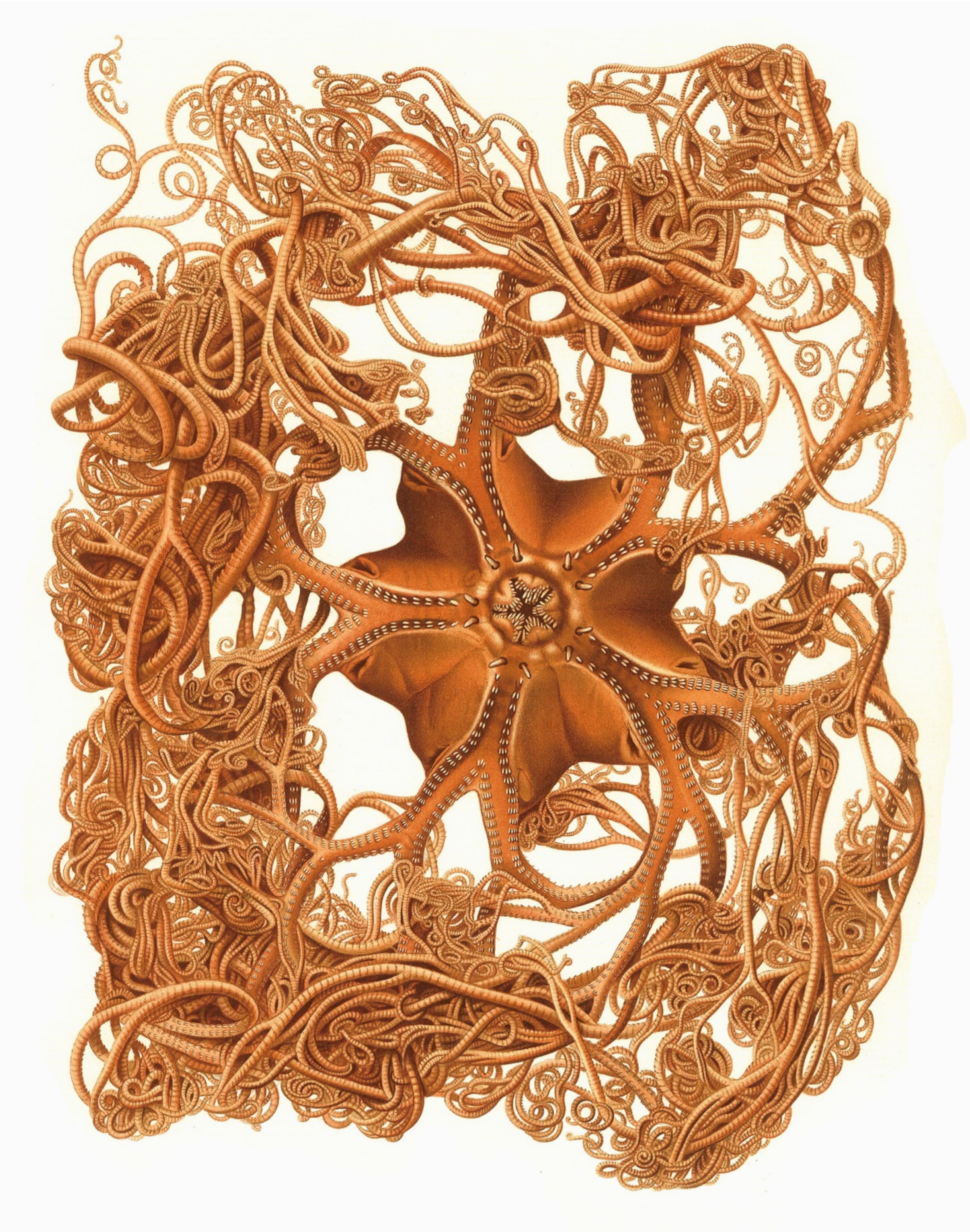

Fig. 1 *Gorgonocephalus arcticus* LEACH, 1819 (from Koehler 1909, pl. 9; as *Gorgonocephalus agassizi* (STIMPSON)). This is the species that was caught during the John Ross expedition.

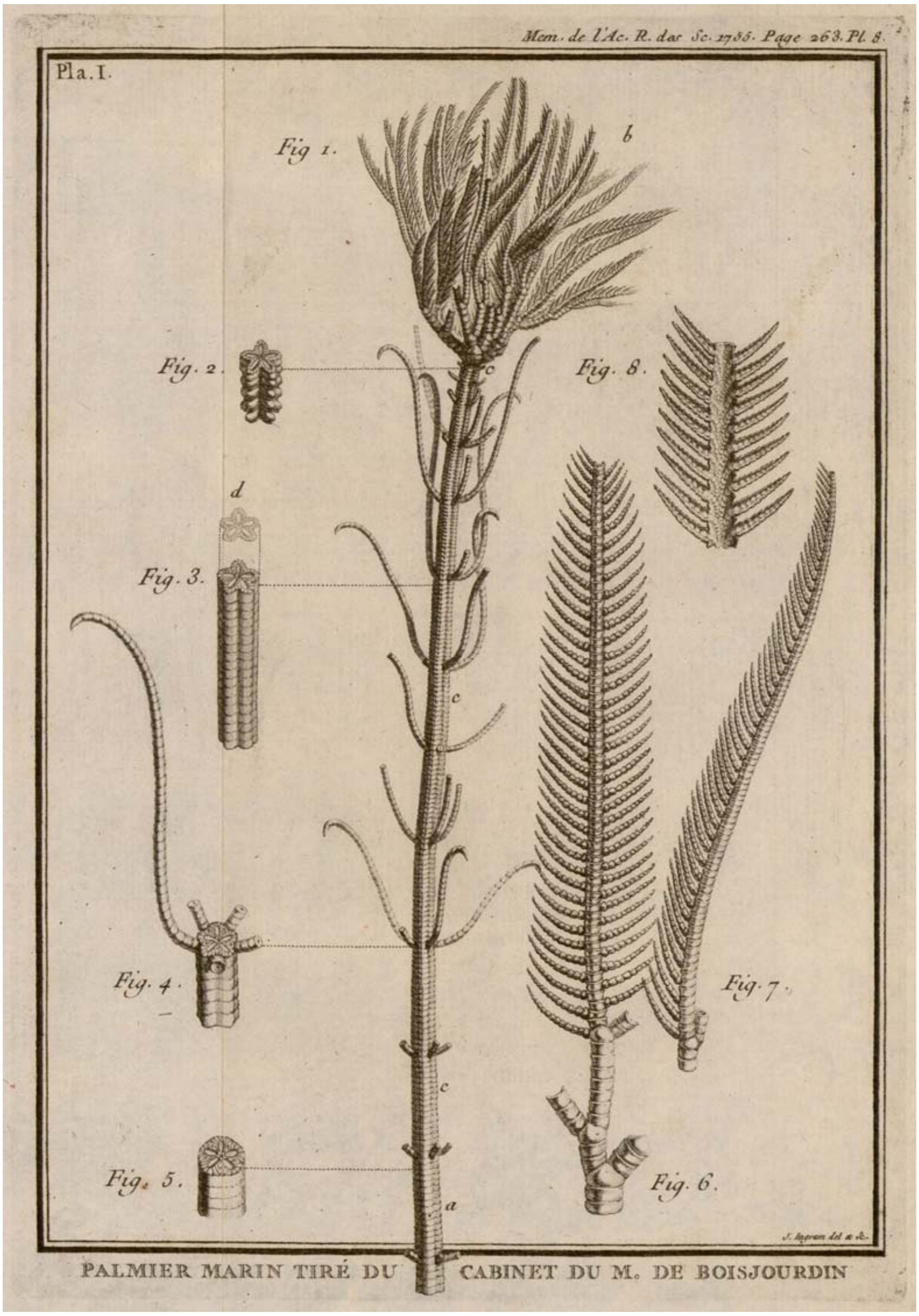

Fig. 2 *Cenocrinus asterius* (LINNÉ 1767) (from Guettard 1761, pl. 8; as ″Palmier marin″). This was the first modern stalked crinoid that was described.

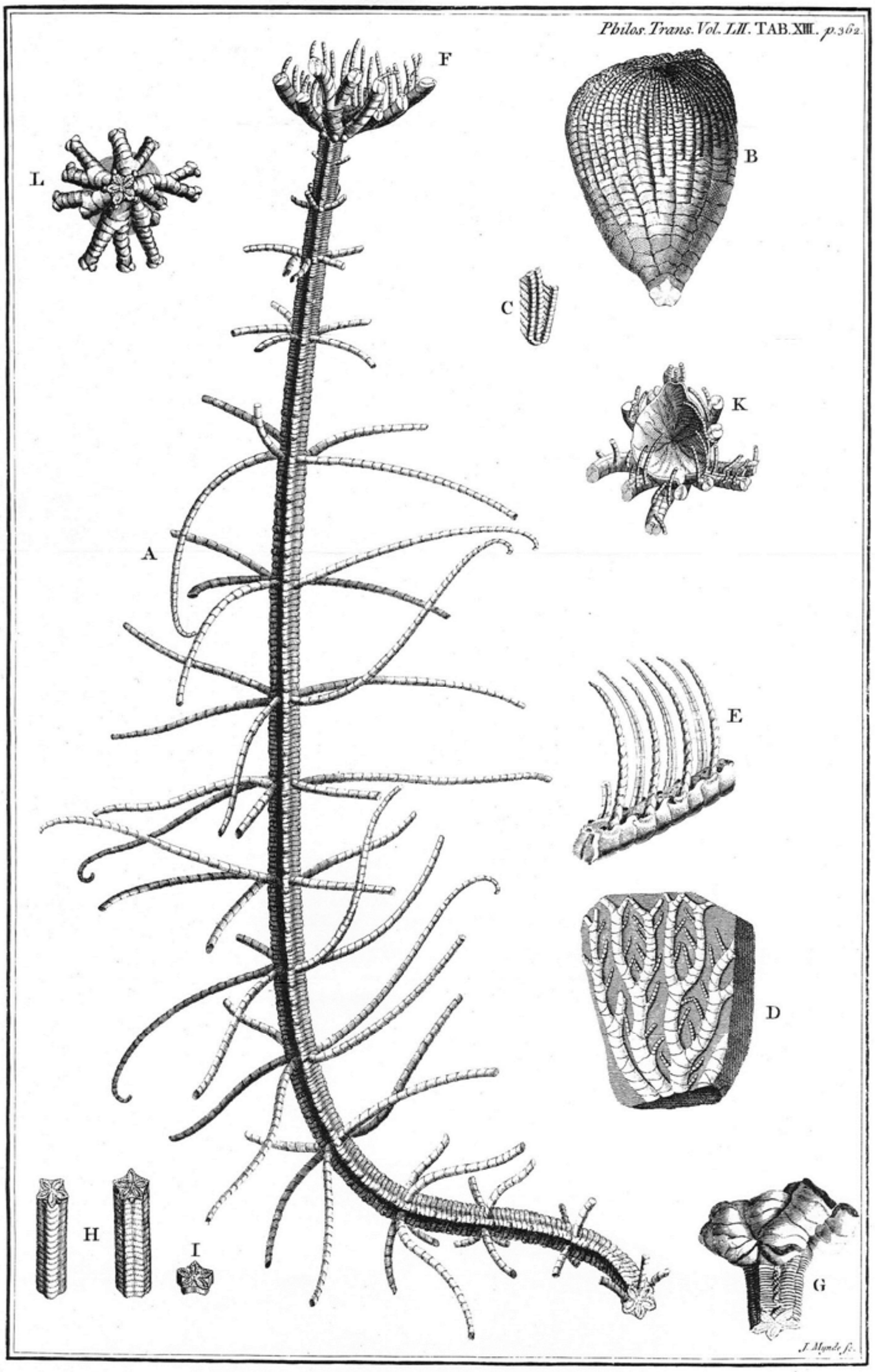

Fig. 3 *Cenocrinus asterius* (Linné 1767) (from Ellis 1762, pl. 13; as ″Encrinus″ from Barbados). This specimen was the second modern stalked crinoid that was described. Also figured are fossil forms: B and C are from the Early Jurassic (Sinemurian) of Pyrton-passage. The site has furnished *Isocrinus (Chladocrinus) tuberculatus* (MILLER) but the drawings are too stylised for proper assignment. D is an indeterminable crinoid copied from Rosinus (1719). G shows the upper part of the stalk and the base of the crown of *Eocomatula interbrachiatus* (BLAKE) from the Early Jurassic (Pliensbachian) of Marston Trussell.

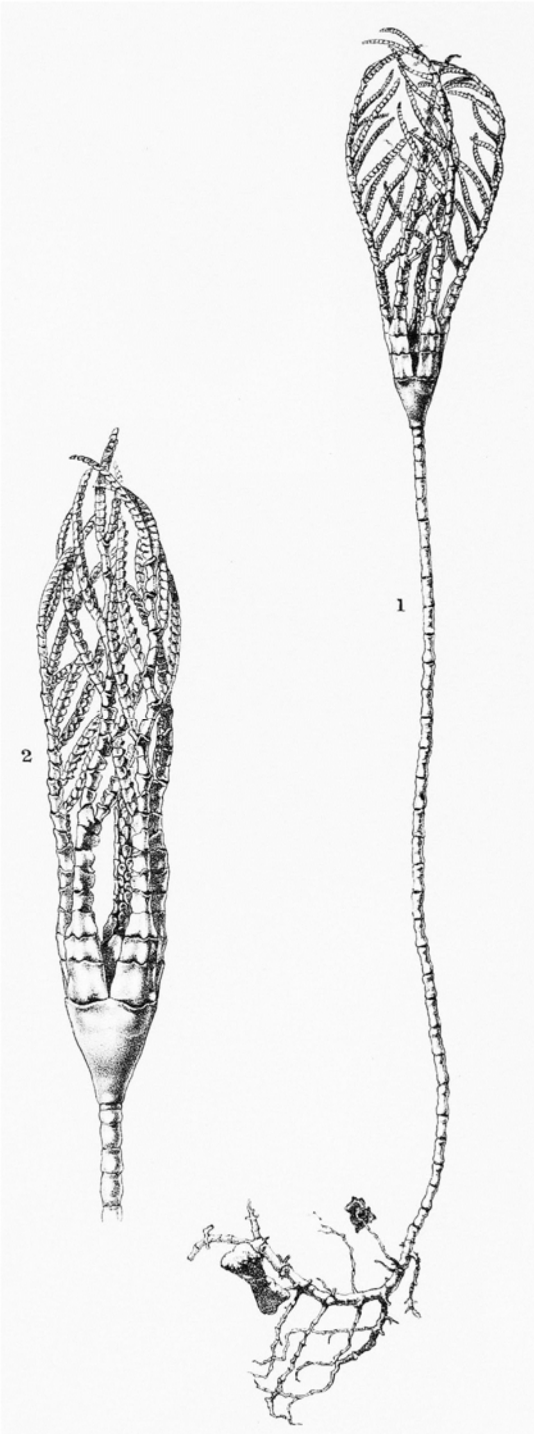

Fig. 4 *Conocrinus lofotensis* (SARS, 1868) (Carpenter 1884, pl. 9, pars; as *Rhizocrinus lofotensis* SARS) from the northern Atlantic.