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THE BIOLOGY AND BIOMINERALOGY OF THE RED CORAL: THE LACAZE-DUTHIERS LEGACY

D. VIELZEUF [1], D. ALLEMAND [2, 3], J. M. SHICK [4], V. ARNAUD [5], S. BODIN [5], L. BRAMANTI [6]*

[1] Aix Marseille Univ, CNRS, CINAM, Marseille France
[2] Centre Scientifique de Monaco, 8 quai Antoine Ier, MC-98000 Monaco
[3] Unité de Recherche de Biologie des Coraux Précieux CSM-Chanel, MC-98000 Monaco
[4] School of Marine Sciences, University of Maine, Orono, ME 04469-5751, USA
[5] Bibliothèque du Laboratoire Arago/Sorbonne Université, Observatoire Océanologique de Banyuls sur Mer, Banyuls-sur-Mer, France
[6] CNRS-Sorbonne Université, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB, Observatoire Océanologique de Banyuls sur Mer, Banyuls-sur-Mer, France
Corresponding author: Daniel.vielzeuf@univ-amu.fr

CORALLIUM RUBRUM
CNIDARIAN
OCTOCORAL
PRECIOUS CORAL
MEDITERRANEAN
SKELETOGENESIS
SCLERITE
RED COLOR
POLYENE
HISTORY OF SCIENCE

ABSTRACT. – In the early 1860s, Henri de Lacaze-Duthiers, Doctor of Medicine and Doctor of Natural Sciences, then a professor of zoology at the University of Lille and later at the École Normale Supérieure in Paris, was entrusted with a mission by the French government to study the Mediterranean red coral (*Corallium rubrum*; Cnidaria; Anthozoa; Octocorallia). Lacaze-Duthiers spent nearly two years at El Kala in Algeria and collected the results of his work in a remarkable book published in 1864 and entitled *Histoire Naturelle du Corail – Organisation – Reproduction – Pêche en Algérie – Industrie et Commerce* (Natural History of the Coral – Organization – Reproduction – Fishing in Algeria – Industry and Trade). We present here a critical review of Lacaze-Duthiers' observations on the red coral with translation in English and quotation of many selected passages augmented by the reproduction of the twenty colored plates appearing in Lacaze-Duthiers' book, with translation in English of the figures' legends. This article is also an opportunity to review the current state of knowledge on the red coral with respect to its anatomy, its reproductive cycle, the mode of formation of its skeleton and sclerites, the chemical composition of its skeleton and the origin of its red color, and finally its ecology.

INTRODUCTION

Henri de Lacaze-Duthiers (Fig. 1) is one of the rare authors of the 19th century whose work on the anatomy, ecology, reproduction and skeleton formation of the Mediterranean red coral is still cited in current publications. As such, he can be considered as the founder of modern science on the precious corals of the genus *Corallium*, both for the results he obtained and the rigor and novelty of his methods.

The Mediterranean red coral (*Corallium rubrum*; Cnidaria; Anthozoa; Octocorallia), from now on referred to as red coral, has been mentioned in the literature for a long time, for instance in ancient texts of Orpheus, Theophrastus, and Pliny the Elder. Orpheus is an omnipresent Thracian bard and musician who may never have existed except in legend. The *Hymns* and *Lithica* (*The Stones*) are attributed to him or his followers, with some pages dedicated to the red coral, a magical stone that would have originated as a delicate plant in the deeps. When this piece was written is uncertain (from the 6th century BCE to the Roman period). Midway between these dates, Theophrastus (b. 372 BCE) wrote succinctly in his *On Stones*, "*Coral, which is like a stone, is red in color and rounded like a root, and it grows in the sea*." The third text, by Pliny the Elder (23 to 79 CE), *Historia Naturalis*, includes details of the mythological origin of red coral, its medical and apotropaic uses and its importance in trade.

Interestingly, the term 'coral' with its etymological antecedents (*korallion* in Ancient Greek from the Orphic tradition and Theophrastus; *corallium* in Pliny the Elder's Latin) refers specifically to the red coral of the Mediterranean. Note that in order to speak about the red coral, Pindar (518-438 BCE) did not use the term '*korallion*' but a locution of four Greek words that can be translated as *'Lily flower of the sea dew*' (Schrader 1901). On the other hand, as noted above, Theophrastus (372-288 BCE) used the term *'korallion*'. This could indicate a date of appearance of the term *'korallion'* between, roughly, 450 and 320 BCE. The term 'coral' (or related) would thus have an age of nearly 2400 years and its use has been limited to the Mediterranean red coral for hundreds of years[1]. The name 'coral' was extended to other species, including the reef-building scleractinians, nearly two thousand years later.

[1] It will be noted that Lacaze-Duthiers does not even bother to use the adjective 'red' to describe the species he studies; for him, 'coral' is 'red coral'.

The etymology of the word 'coral' is still discussed, perhaps coming from the Greek and Latin root words for antler (Gr. *kéras*, Lat. *cornu*) (Poplin 2000). In another putative origin, *korallion* would have its roots in *koréô* (I adorn) and *hals* (the sea) as a beautiful marine production (Roquefort 1829). The word might be also a derivation of *korê halos*, '*daughter of the sea*' (Schrader 1901, p. 457, Chantraine 1968). In the absence of a consensus, we prefer here the last and most poetic etymology '*daughter of the sea*'. Interestingly, the red coral would be at the same time a daughter of the sea and the mother of all corals, at least from an etymological point of view.

Long after the publication of Lacaze-Duthiers' monograph in 1864, the red coral has been the subject of an upsurge in scientific publications since 2000. This interest is due both to the place that the red coral holds in jewelry and to its importance in the fields of marine ecology, environment or materials' science, as well as the new threats that its populations are experiencing in recent years in the face of climate change (Pérez *et al*. 2000, Garrabou *et al*. 2001, Bramanti *et al*. 2005). Concerning the environment, red coral grows slowly and its annual growth rings contain information on past environmental conditions (*e.g.*, Ricolleau *et al*. 2019). In this context, and on the bicentenary of his birth in 1821, it is interesting to review the results of Lacaze-Duthiers published more than 150 years ago, to identify the many points where his observations proved to be accurate and fruitful, still innovative but not always acknowledged. Despite the relatively short duration of his missions (less than two years in total) and the rapid publication of his monograph (less than four years since the launching of his mission), Lacaze-Duthiers addressed many questions: history of knowledge, anatomy, skeletal formation, growth rate, reproduction, taxonomy, fishing methods, and fishery regulation. Here we will only deal with the aspects of general biology, anatomy, reproduction, skeleton formation and growth rate, and briefly with ecology and fishery.

It is interesting to note that Lacaze-Duthiers was sensitive to scientific controversies and denounced "*the habit that men have of repeating things without verifying their accuracy by themselves*" (HLD, p. 4)[2]. Strangely enough, this perceived shortcoming has been repeatedly applied to his own work over the years, some of his results being reported in an erroneous or incomplete way, particularly in the literature in English; this is another reason for a detailed review of his work. In the following pages, we shall endeavor to show the richness of Lacaze-Duthiers' observations, some of which have never been duplicated, others of which have not yet been considered by the community, and to clarify some contentious points. As importantly, we will review the current state of knowledge on the reproduction, organization and ecology of the red coral.

HISTORICAL CONTEXT OF LACAZE-DUTHIERS' STUDY

Lacaze-Duthiers was entrusted with a study mission on the red coral in Algeria by Mr de Chasseloup-Laubat, Minister of the Navy and the Colonies, on the recommendations of Pr de Quatrefages, who held a chair at the National Museum of Natural History in Paris. For the French government, this mission had an obvious economic goal. Indeed, the introduction of Lacaze-Duthiers' monograph begins with this sentence: "*Since France occupied Algeria, there is perhaps no administrator who has not understood that Coral can become a source of wealth for our colony*" (HLD, p. 13), and further on "*to use a natural product… for an average value of 2 million* [French francs of that time]*, and which represents in trade… the enormous sum of 10 to 12 million*[3]" (HLD, p. 343). The flourishing coral trade in Algeria – about 30 tons fished in 1860 (HLD, p. 324) – was conducted by Italian fishermen and the products shipped to Italy (Napoli, Livorno or Genoa). No Frenchmen were involved in this activity, which represented an economic loss for France.

Interestingly, Lacaze-Duthiers did not address the issue from a simple technical, or even resource assessment, perspective. For Lacaze-Duthiers "*a legislation on fishing, whatever its nature, in order to be serious, must be based on scientific data, especially on those related to reproductio*n" (HLD, p. 14), a surprisingly topical statement. Thus, Lacaze-Duthiers assigned to himself the objective to establish "*the time, the mode of reproduction and the conditions favorable or harmful to the coral fishery…"* to provide *"… serious data to the administrators in charge of making the regulations preventing the depletion of the* [coral] *banks"* (HLD, p. 18). However, the mission of Lacaze-Duthiers was not only focused on biological questions. He made a real sociological study of the coral fishing profession, fishing regulations, coral trade and of the links between fishing and colonization. He made proposals to change regulations, and more broadly to

[2] Page 4 of Lacaze-Duthiers' monograph. HLD is an abbreviation used throughout our text. There is no English version of his original French text and the present translation in English of HLD's text and captions is ours.

[3] As an indication, the purchasing power of 1 Franc in 1901 would the same as that of about 400 € in 2021. Source: https://www.insee.fr/fr/information/2417794. However, this figure seems extravagant: as another estimate, HLD obtained 3000 Francs in 1873 to rent a furnished house (1200 Francs) at Roscoff (Brittany, France), buy a small boat (210 Francs), pay for the travel expenses of young workers, and hire the service of two sailors for one year (A. Toulmond, pers. comm. and C Jessus & A Toulmond 2022). We estimate that 100,000 € would be in 2021 a maximum sum to cover the same expenses, translating into 1 Franc in 1873 equivalent to about 30 € in 2021.

Fig. 1. – Henri de Lacaze-Duthiers in a study aquarium at the Arago Laboratory in Banyuls-sur-Mer (France), in 1895, studying and drawing fragments of cold-water corals: *Dendrophyllia ramea* (large piece in the background) and *Madrepora oculata* (small piece in the foreground). (Lartaud & Menot 2021). Collection of the library of Arago Library/Sorbonne Université.

make coral fishing more efficient, more sustainable, and more humane for the fishermen: "*The mission with which I had the honor of being entrusted had as its main aim to find out whether the coral banks were not depleted by too active and continuous fishing, whether it would not be possible to develop them in such a way as to increase the quantity and value of the products*" (HLD, p. 266). He also details with sympathy the difficulty of the work of the coral fishermen, which involved turning the large capstan to deploy, maneuver, and retrieve the massive *ingegno* (St. Andrew's cross), and in the absence of wind even rowing the 12-16 tons' boat: "*To judge the efforts and fatigues of these unfortunate men, one must have spent several days on board: then one will have an exact idea of what the state of a coral fisherman really is. The sailors are almost naked, they keep only their pants. Their burnt skin, blackened by the sun, gives them a rough and foreign physiognomy; they sing, however, to encourage each other… Then these unfortunate men, panting, are sad to behold: the heat of the sun which burns them makes their bodies stream with sweat, their eyes are bloodshot; their face, despite its swarthy tint, reddens sharply; the veins of their neck, swollen and protruding, show all the power, all the energy of their action*" (HLD, p. 238-239)[4].

The mission in Algeria entrusted to Lacaze-Duthiers began on October 1, 1860, and was planned to last one year. Lacaze-Duthiers quickly realized that this time was too short to answer the questions asked. He therefore decided to extend the duration of his mission by requesting a leave of absence at his own expenses. He returned to Algeria during the spring, summer and fall of 1862. The results of his three field seasons are recorded in an exceptional 371-page book published in 1864, containing twenty color plates and entitled *Histoire Naturelle du Corail – Organisation – Reproduction – Pêche en Algérie – Industrie et Commerce* (Natural History of the Coral-Organization-Reproduction-Fishing in Algeria-Industry and Trade) edited by Jean-Baptiste Baillière et Fils, publisher of the Imperial Academy of Medicine.

[4] In the same decade that Lacaze-Duthiers did, the Catalan utopian socialist and inventor Narcís Monturiol also recognized the dangerous life of red coral fishermen (including helmeted divers) at nearby Cape Creus (Spain). In response, Monturiol conceived and engineered a submarine intended to study the undersea and safely exploit its resources, including precious coral (reviewed in Shick 2018, p. 173-176). Despite successful sea trials, the submarine *Ictíneo* never saw commercial usage and the venture failed from lack of funds.

HISTORY OF KNOWLEDGE AND METHODS OF OBSERVATION

Lacaze-Duthiers' book begins with a historical synthesis of knowledge on the biology of red coral and the notion of animality of coral: "*By following this path, we will draw valuable lessons from the study of the history of science*" (HLD, p. 2). Starting with the bloody origin of red coral (the myth of Perseus and Medusa) and Ovid's *Metamorphoses*, Lacaze-Duthiers details the progression of ideas that have led to the classification of coral among animals: "*Placed successively in each of the three kingdoms of nature, it offered… characters that were completely opposed to those who saw in it a mineral, a plant or an animal*" (HDL, p. 2). Lacaze-Duthiers gives a special place to the work of Jean-André Peyssonnel and his attempts to have his opinion (that the red coral belongs to animal kingdom) recognized. Peyssonnel's work was finally presented to the Royal Society of Science of London on May 7th, 1752 (Faget & Vielzeuf 2018) and published in England[5]. Lacaze-Duthiers points out that "*It is therefore probable that, on withdrawing from the French scientific world, he* [J A Peyssonnel] *turned his eyes for some time to another country; then, abandoning himself entirely to that discouragement which inevitably accompanies injustice, he ceased to work*" (HLD, p. 19)[6]. This historical chapter ends with an empathetic description of the life of Peyssonnel: "*Peyssonnel was not fortunate. His devotion to his fellow citizens during the great plague of Marseille, his generous and liberal offer for the foundation of a* [annual] *prize* [for outstanding results in marine science, rejected by the Academy of Marseille]*, and above all his great discovery, should have given him, in his own country, a position that would have kept him in science; and today France would not have to regret having rejected a great and fertile scientific idea, having neglected a man who does her honor, and above all having allowed the date of a great discovery that belonged to him to be marked by publications in England*" (HLD, p. 19).

Before presenting the anatomy of the red coral, Lacaze-Duthiers provides a sort of instruction manual for naturalists to obtain and observe living red coral. According to him, it is the longstanding difficulties of observing living coral that are the "*causes of the long ignorance in which we have remained*" (HLD, p. 37). The details he provides constitute a veritable Materials and Methods for his work to become a real textbook: "*I also wish that other naturalists could more easily, with these indications, verify the facts I present and push the observations further*" (HLD, p. 37). In order to observe living coral, Lacaze-Duthiers developed innovative experimental protocols: "*the coral must be suspended halfway up the vase and attached on the root side by a wire to a small, easily moved metal hook*" (HLD, p. 38; see our Fig. 2A, B). "*The coral* […] *freely suspended, swinging in the moving water, at first contracts, or even does not close, but always soon blossoms after the renewal of the water*" (HLD, p. 39, and also pl. XII, fig. 61), a method classically used nowadays in our laboratories (*e.g.*, Ferrier-Pagès *et al*. 2005 and our Fig. 2). Lacaze-Duthiers also notes the importance of water quality and temperature. Regarding the water, Lacaze-Duthiers indicates "*If we take the water in a port, we must move away as much as possible from the buildings, in order to be more assured of its purity. In La Calle* [now El Kala]*, the water was drawn from the harbor, almost under the lighthouse, but during the hot weather, it was taken from outside with a boat. Here, in this respect, is an interesting observation. A coral colony that had already lived for a long time very well… suddenly saw its polyps closing for two weeks; the water, which was renewed with the greatest care, was taken from the pier, not inside, but outside the port. The sailor Lanceplaine … who has always taken care of my aquariums with such great zeal and intelligence, thought that this water was too rough, and he went to draw some from inside the port: the polyps then blossomed and became superb. Is it not natural to think that the wave, breaking every moment on the rocks, provided a very aerated water, quite different…from that of the depths where the coral lives?* (HLD, p. 39 and 40). The importance of water temperature also considered by Lacaze-Duthiers will be discussed later, in the 'Ecology' section.

ANATOMY

Lacaze-Duthiers' contribution (pl. I to VII) and current state of knowledge

Lacaze-Duthiers provides the first detailed description of the anatomy and histology of red coral. His work remains relevant because modern anatomical or histological studies on *Corallium* species are still rare (Grillo *et al*. 1993, Nonaka *et al*. 2012). He begins this chapter by defining the anatomical vocabulary[7]: coral is defined

[5] *Transactions philosophiques de la Royal Society de Londres* pour les années 1751-1755, Paris, 1756, p. 54.

[6] To put Lacaze-Duthiers' empathy with Peyssonnel in historical context: nearer the time, Buffon (1749) had set the record straight, as later (1838) Flourens did (Refs and discussion in Shick 2018, p. 55).

[7] Glossary:

Axis: red hard part of the coral used in jewelry. Instead Lacaze-Duthiers used the words 'skeleton' or 'polypier'.

Bark: Lacaze-Duthiers uses this term to refer to all tissues surrounding the axis (*i.e.*, coenenchyme (sarcosome) and polyp).

Blastogenesis: Lacaze-Duthiers created the word 'blastogenèse' associating two Greek words meaning bud and origin, in other words 'birth by bud'. It is synonymous of 'asexual reproduction'.

Blastozooid: (HLD: blastozoïte). Association of two Greek words bud and animal, in other words polyp deriving from a bud. Synonymous with clone. Opposed to oozoid (oozoïte).

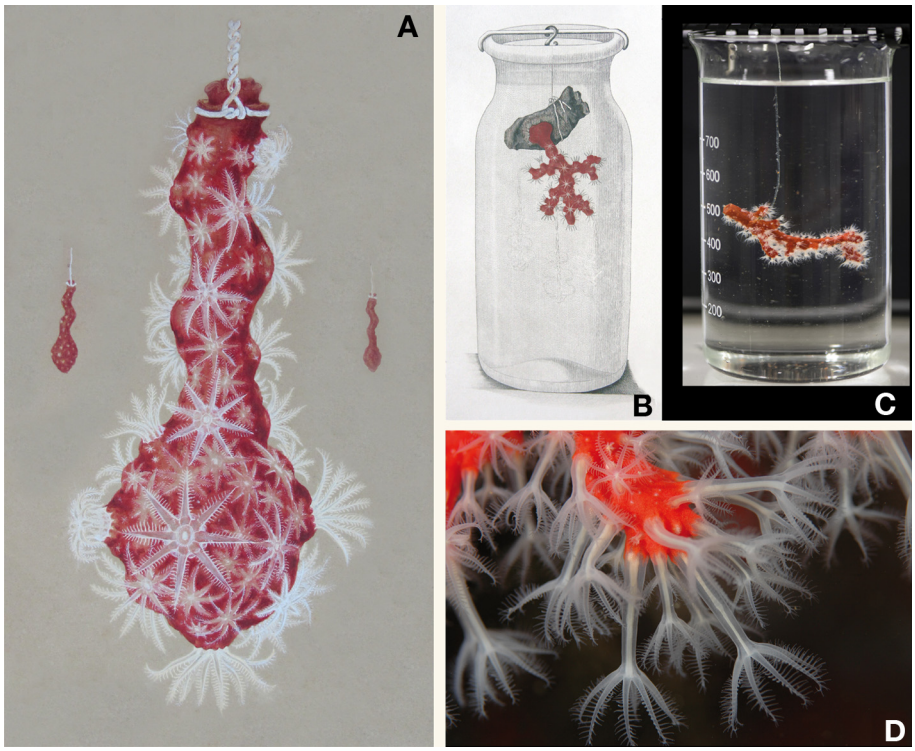

Fig. 2. – **A**: Original of a Lacaze-Duthiers' watercolor plate (Collection of the library of Arago Library/Sorbonne Université). This watercolor shows the chain by which the coral branch was suspended in a glass jar. **B**: It is with this device and a horizontal microscope that Lacaze-Duthiers made his observations in the laboratory; observation on site being impossible at the time. Some of the observations were also made on samples brought back from the sea, still attached to their substratum. **C**: Present-day culture of red coral at the Scientific Center in Monaco (CSM) (Photograph: G Loentgen). Note the similarities between B and C. **D**: Coral branch with its polyps deployed photographed on site (photograph: R. Graille). Modified from Faget & Vielzeuf (2018).

as "*an aggregation of animals united by a common tissue deriving from a first being* [primary polyp] *by means of budding*" (HLD, p. 22). The polyp is referred to as "*a single animal… resembling by its external characters the one born from an egg or a bud*" (HLD, p. 23). Colonial budding corresponds to the process of blastogenesis[7], used here in the sense of reproduction via budding. The zoanthodeme [coral colony] corresponds to "*the whole of everything that makes up the most complete branch, soft, hard and animal parts*" (HLD, p. 23). This whole is made up of two parts: "*one central, hard, brittle, of a stony nature… which is used in jewelry; the other, external, similar to a soft, fleshy bark that is easy to cut with the fingernail when it is fresh, and powdery when it is dry: this is the living animal layer formed by the polyps*" (HLD, p. 24). This second part, which Milne-Edwards & Haime (1857) called "polypièroïde", Lacaze-Duthiers proposes to call sarcosome[7] (fleshy body). Although the term 'sarcosome' is occasionally used today (*e.g.*, Fürst *et al*. 2016), the term coenenchyme is preferred (see DeVictor & Morton 2007) and will be used from now on. We will refer to the central, hard part of a stony nature as the axis (and sometimes skeleton or axial skeleton).

Then, Lacaze-Duthiers describes the general morphology of a coral colony. He recognizes that the "*shape and arrangement of the branches depend very much… on the conditions in which they have developed*" (HLD, p. 26): "*a relatively considerable development in length*" on the coasts of Africa, a "*short and stocky*" coral on the coasts of France (HLD, p. 26). It is known today that many factors affect the growth and shape of red coral colonies (Montero-Serra *et al*. 2015, Kahramanoğulları *et al*. 2019) as well as reef-building corals (Todd 2008). However, to our best knowledge, although there is a relationship between the shape of a colony and hydrodynamics, no clear relationship is established between the shape

Coenenchyme: a term that Lacaze-Duthiers never used. Instead he used the word 'sarcosome'. Throughout the text and the figure captions, we replaced the word 'sarcosome' with 'coenenchyme'.

Oogenesis: Lacaze-Duthiers created this word (Oogénèse) by association of two Greek words: egg and origin (birth by egg).

Oozoid: (HLD: oozoïte) from Greek egg and animal. Polyp deriving from an egg. Opposed to blastozooid.

Polypier: a word used by Lacaze-Duthiers for 'axis'.

Puntarella: Lacaze-Duthiers used (rarely) this term in the sense of 'small pointed thing" or tip of a coral branch.

Sarcosome: a word invented by Lacaze-Duthiers by the association of the Greek words: flesh and body (fleshy body) referring to the living tissues surrounding the mineral red axis. He used this term in the sense of coenenchyme. In most cases (but not always) Lacaze-Duthiers considers that the polyps do not belong to the sarcosome (coenenchyme).

Sclerites: small grains of magnesian calcite in the coenenchyme and sometimes at the base of the polyps. (Synonymous with spicule).

Spicule: (see sclerite): A word that Lacaze-Duthiers used for 'sclerite'.

Zoanthodeme: Lacaze-Duthiers created the word zoanthodème from the Greek words animal, flower and people (population of animal-flower). It is used in the sense of an entire red coral colony, sometimes a young colony not yet branching, or often the branch of a larger colony.

(and color) of the coral and its geographic origin. In other words, it seems to us difficult to differentiate a coral from North Africa from those of Southern France, although some coral traders and coral fishermen state that they can do it (M Palomba, T Garcia Fuentes & C Di Domenico pers. comm.).

Lacaze-Duthiers then notes that "*the coenenchyme* [sarcosome] *is swollen into a club and has a larger diameter at the tips than in the lower part of the stem. This is because blastogenesis is and must be very active towards the tips, since it is responsible for the increase in length*" (HLD, p. 28). "*The distribution of the polyps on a branch is nothing special, any more than the number; both depend absolutely on the activity of blastogenesis of the whole zoanthodeme, or of one of its parts. Thus, the more polyps a branch bears, the more important is its increase in length; as for the increase in diameter, it is obviously related to the power of assimilation of the dissolved matter contained in the nourishing liquids* [delivered by the internal system of canals]. *It is in the growing extremities that the polyps are the most numerous and the most closely packed*" (HLD, p. 53).

Lacaze-Duthiers also describes the morphology of a coral branch: "*A branch that is alive and well and in a good state of well-being when taken out of the water, is strongly contracted and covered with prominent bulges surrounded by folds and grooves at the bottom. Each bulge corresponds to a polyp and has at its top eight folds radiating around a central pore which has the appearance of a star. It is this pore that, opening and dilating little by little, lets the polyp out*" (HLD, p. 45 and Fig. 4 in pl. I, (see also Nonaka *et al*. 2012, their fig. 15, for *Pleurocorallium elatius*)). Lacaze-Duthiers then describes the anatomy of the polyps and their relationship with the other tissue, *i.e*., the coenenchyme: *"…the body of a polyp presents like a bag whose lower part has its own walls merged with the bark* [coenenchyme]*, while the upper part is elongated into a transparent tube, crowned by eight fringed arms* [tentacles]*, and in the cavity of which the blades* [mesenteries] *arising from the circumference delimit circularly symmetrical chambers"* (HLD, p. 65). "*But in a branch or zoanthodeme, the animals are inserted in the common tissue that covers the axis*" (HLD, p. 65). This *"fleshy body… which is so often called bark*" (HLD, p. 66) has varying thicknesses, which are *"as a direct result of the activity of blastogenesis*" (HLD, p. 66). Note that Lacaze-Duthiers did not recognize the existence of two types of polyps in the red coral, the autozoids (those described by Lacaze-Duthiers) and the siphonozoids[8] (see Nonaka *et al*. 2012).

[8] Siphonozoids are regressed polyps playing a role in the intake and release of water. This type of polyp is observed in the red coral (P. Ganot, CSM, pers. comm.), but to our knowledge this has not yet been mentioned in the literature.

Lacaze-Duthiers continues on the anatomy of the coenenchyme: "*In a thin section of its tissue, the microscope reveals first of all very small, brightly colored crystalline masses, scattered here and there, and to which the name of spicules, sclerites or calcareous corpuscles has been given; then numerous canals some larger, others smaller, crisscrossed in all directions; finally, a general common tissue, in which the canals are hollowed out and the spicules scattered*" (HLD, p. 69, Fig. 18 in pl. IV). "*By pushing the anatomy further, it is easy to recognize that there are canals of two very different orders; some, very regular, relatively very large and lying on the axis, are joined together in a deep layer of parallel tubes; the others, very irregular and much smaller than the former, form an unevenly meshed network and occupy the entire thickness of the bark* [coenenchyme]" (HLD, p. 76, Fig. 21 in pl. V). These canals (Fig. 4A) correspond to what modern zoologists call the gastrovascular system of endodermal origin. This description is still relevant and has rarely been redone in greater depth since then (see for example Grillo *et al*. 1993, their Fig. 3A). For Lacaze-Duthiers, the large canals parallel to the skeletal axis "*lie immediately above the axis*"[9] (HLD, p. 77). These canals are "*applied immediately to the axis, the latter, as it solidifies, retains their imprint*" (HLD, p. 78). Lacaze-Duthiers did not have the proper tools to observe that between these large canals and the skeleton a cell layer, similar to the calicoblastic epithelium of the scleractinian corals, is present and generates the axial skeleton. This cell layer was discovered almost 130 years later by Grillo *et al*. 1993 (see also the review in Allemand 1993). Then, Lacaze-Duthiers perfectly describes the relationships of these different canals with each other and with the polyps: "*The large parallel canals never seem to abut directly through orifices as large as themselves with the polyps*" (HLD, p. 78). "*The two networks terminate directly by a very large number of anastomoses*" (HLD, p. 79). Lacaze-Duthiers also describes the histology of these canals: "*All canals, large and small, deep or superficial, have constantly the same intimate texture; their interior is lined by a more or less thick layer of cells, analogous to those which have been seen to form the inner lining of the walls of the barbules* [pinnules] *of the arms* [tentacles] *and of the general cavity*" (HLD, p. 80). Lacaze-Duthiers' vision is perfect: these two cell types have the same embryological origin (Tixier-Durivault 1987). It should be noted that a precise histology of these canals in the Octocorallia is still missing.

Lacaze-Duthiers then looked at the role of these canals: "*It is now easy to see the circulation of the nutrient fluids throughout a coral zoanthodeme*" (HLD, p. 81). We note that Lacaze-Duthiers has understood the role of digesta in the nutrition of the colonial coral (see Picciano & Ferrier-

[9] Rather than 'axis', Lacaze-Duthiers uses the term 'polypier'.

Pagès 2007)[10]. He compares this nutrient to milk: "*The milk* [obtained after tearing the tissues of a living colony] *is a veritable emulsion in which the constituent elements of both the polyps and the coenenchyme enter; it is the nourishing fluid that has escaped from the vessels that contained it*" (HLD, p. 84). The composition of this fluid has never been further studied.

To study the internal histological structure of the tentacles, Lacaze-Duthiers had the idea of everting the tentacle so that the internal cell layer was outside (HLD, Fig. 13 in pl. III), an idea taken up much later by modern researchers to study the transport properties of sea anemone tentacles (Bénazet-Tambutté *et al*. 1996a). From these observations, Lacaze-Duthiers highlighted the histological difference between the two cell layers composing the tentacle: "*There are two very different layers of tissue in the walls of the arms* [tentacles]". He observes that, in contrast to the outer cell layer, the cells of the inner layer are not firmly attached to each other: "*The great ease with which these cells detach themselves*" (HLD, p. 60). This property of the endodermal cell layer of Anthozoa is now well established and is used in some experimental set-ups (Bénazet-Tambutté *et al*. 1996b).

Lacaze-Duthiers recognized that the coenenchyme is covered by a film, now described as the oral ectoderm: "*There is an excessively thin layer on the outside of the coenenchyme, which, although it has no structure, nevertheless seems to be a peculiar epidermal production, probably due to the cells which form the first layers…*" (HLD, p. 90). Most of Lacaze-Duthiers' descriptions and drawings can be found in subsequent zoological treatises, both early (Claus 1884, Delage & Hérouart 1901, Perrier 1936) and more recent (Grassé *et al*. 1970).

Summary concerning the anatomy

1 – The red coral colony comprises a central hard skeleton (the axis) surrounded by soft organic tissues (the coenenchyme), in which the polyps, with eight tentacles and mesenteries, each are lodged.

2 – The coenenchyme consists of (1) an epithelium, immediately above the axis, (2) a deep network of large canals, located in the grooves of the axis, (3) a more superficial network of smaller canals connected with the deep canals and the polyps, (4) the mesoglea (an amorphous and practically acellular extracellular matrix located between the ectoderm and the endoderm [gastroderm]), (5) a superficial epithelium.

3 – Sclerites are located in the coenenchyme and more rarely in the polyps.

[10] Nevertheless, red coral, like most marine invertebrates, is also capable of absorbing amino acids directly from seawater through its external epithelium with an affinity below the micromolar level (Allemand & Bénazet-Tambutté, unpubl data).

THE RED CORAL REPRODUCTIVE CYCLE

Lacaze-Duthiers' contribution (Plates IX to XVI)

In the first part of this section, we will report as accurately as possible the results obtained by Lacaze-Duthiers, without reference to current knowledge. In a second step, we will comment on these observations, based on the present state of the art. Lacaze-Duthiers claims to be the first to observe red coral reproduction (HLD, p. 175). He sees six main periods in the early stages of development of the coral (1) ovarian period, (2) period of free-living larva, (3) metamorphosis and attachment of the larva, (4) formation of the complete polyp, (5) appearance of new polyps in the colony, and finally (6) development of the skeleton.

Lacaze-Duthiers starts his study by describing the reproductive male and female organs of coral, observing for the first time the presence of male organs (HLD, pl. IX). Then, he noted that colonies are most often either male or female: the coral is therefore mostly unisexual (gonochoric[11]). Lacaze-Duthiers notes, however, that in certain colonies, both male and female polyps can be found, and the colony is then considered bisexual (hermaphrodite). In this case, either the male polyps are carried by one of the branches and the female polyps by another, or they are mixed. Lacaze-Duthiers also reports rarer cases where the reproductive organs of both sexes are present in the same polyp, resulting in a characterized hermaphroditism (HLD, p. 126 and 144, pl. XI). As we will see later, some of these observations are debated.

At the beginning of the reproductive period, by the end of spring, the male polyps emit through the mouth a white liquid, which contains numerous spermatozoa, among other substances (HLD, p. 146). The fertilization of the egg (here synonymous with oocyte) takes place not only in the cavity of the polyps, but even deeper in the ovary. The eggs develop into embryos inside the polyps. The red coral is thus viviparous (HLD, p. 151). After detaching from the ovary, the fertilized egg remains in the polyp's cavity until it has developed sufficiently to live an independent life. The egg is spherical at first and becomes ovoid as an embryo. Then it lengthens and takes the shape of a small worm: it becomes a larva.

Although well developed, the larva remain a long time in the general cavity of the polyps (HLD, p. 152). Shortly after, when it exits the ovary (never at an egg or embryonic stage but as a larva), its length is 1.5 to 2 times its width, then at the end of the free-living period it is 15 times longer than broad (HLD, p. 160). Lacaze-Duthiers was unable to determine the duration of brooding because he did not know at what exact time the fertilized eggs

[11] Gonochorism is a sexual system where there are only two sexes and each individual organism is either male or female (King *et al*. 2006).

detached from the ovary to begin their embryonic development. However, Lacaze-Duthiers estimated this period to last one month.

It is via the mouth of the female polyp that the larvae escape. Lacaze-Duthiers assisted many times in the release (or birth) of coral larvae, often even provoking it[12]. This release takes place when the polyp is contracted as well as when it is expanded. The mouth opens widely, and the larvae come out sometimes as a result of their own vibratory movements, sometimes expelled by the contractions of the female polyp (HLD, p. 153, pl. XIII). At the end of August, and especially at the beginning of September, the release of larvae takes place in a constant and continuous way until September 15; from this date the number of births decreases, and in October, but especially in November and December, they cease entirely. Thus, the period of reproduction extends from spring to the beginning of autumn and ceases during the winter. The number of births is greatest in late summer (HLD, p. 156).

After its exit from the polyp, the larva starts its metamorphosis by forming a cavity at its surface and covering itself with vibratory cilia (HLD, p. 161, pl. XIV and XV). Its tissues begin to differentiate, including a change in the proportion of its two extremities: one becomes larger and broad, the other more pointed, and on the latter an opening is formed which will become the mouth (HLD, pl. XV). The bigger part will become the basal end, while the pointed part will become the oral part. In water, larvae move "backwards" (mouth behind) (HLD, p. 166). Lacaze-Duthiers notes that in the aquarium tanks the larvae tend to swim upward, to the surface and the author relates this observation to the fact that, consequently, coral colonies often develop on the roof of caves and cavities. Then, the larvae change shape: from elongated they become discoid and adherent (the base seems to be covered with mucous matter which could contribute later to its adherence to the substratum). The basal face is flat, and the other one is hollowed out by a depression surrounded by a bulge (on which the eight tentacles will develop): it is the mouth. The transformation goes quickly (a few hours) and it is often related to a change in weather conditions (hot wind). Some larvae metamorphose without attaching to the substratum, others after attachment on a support (HLD, p. 164). In aquarium tanks, the metamorphosis of the larvae occurs 10 to 15 days after release, but Lacaze-Duthiers is convinced (without more precision) that this period could be shorter at sea.

Lacaze-Duthiers observed that the embryos or larvae never contain sclerites (HLD, p. 173). The sclerites appear shortly after the larvae are attached and the tentacles begin to form. The next steps of development are closely linked to the formation of the skeleton, and thus they will be considered in the skeleton section below.

Another important aspect must be addressed here. The first polyp that forms is the result of sexual reproduction and is called the founder, or primary, polyp. Then, quickly, new polyps, which are not a result of sexual reproduction, appear on the nascent colony. Lacaze-Duthiers speaks about 'blastogenesis', a concept defined above. According to Lacaze-Duthiers this asexual reproduction is a remarkable and exceptional property in the animal kingdom (HLD, p. 90). It is immediately after the development of the first polyp that one or more new polyps appear; these are called 'blastozooids' or 'daughter polyps', although the latter has no connotation of their sex. At the beginning, the new polyps appear in the tissues of the coral in the form of small white buds pierced by a hole in their center. In some cases, they are arranged regularly in circle around the older polyps (HLD, p. 96). The small white bud communicates with the canals of the coenenchyme and has a star shape and presents at its circumference eight white lines or indentations (HLD, p. 97 and 98). Then, on the edge of the orifice, representing the mouth, small bulges appear and lengthen gradually and eventually become tentacles of the new polyp. From the beginning, these nascent tentacles appear in the number of eight, and a little later, they become covered with pinnules. Quite quickly the buds reach the size of the adults. This is how the polyps multiply at the beginning and then throughout the life of the colony, contributing to its growth. Later in the development of the colony, Lacaze-Duthiers notes that the cloning (or budding) of polyps occurs all over the colony but especially at the tip of the branches in the zones that surround the older polyps (HLD, p. 91). To return to the beginning of the colony's development, Lacaze-Duthiers asks the question of the fate of the first polyp: is it positioned in the middle, above or below its clones? (HLD, p. 183). Lacaze-Duthiers does not answer this question which also raises the question of the life span of a polyp that would only be answered more than 150 years after Lacaze-Duthiers' work (see below).

Current state of knowledge

The study of the red coral reproductive cycle is probably the most thorough part of Lacaze-Duthiers' work. Since then, the reproductive cycle of *C. rubrum* has been studied by various authors (*e.g.*, Vighi 1972, Santangelo *et al*. 2003, Torrents *et al*. 2005, Tsounis *et al*. 2006, Viladrich *et al*. 2016, 2017). Most of the studies focused on oogenesis and reproductive effort, while studies on larvae have been sporadic, at least before the last decade (but see Weinberg & Weinberg 1979), during which an increase in the number of studies on larvae is observed (Martinez-Quintana *et al*. 2015, Zelli *et al*. 2020, Guizien *et al*. 2020, Viladrich *et al*. 2022). Most of Lacaze-Duthiers' observations are still valid and many of them,

[12] To our knowledge, Cavolini (1785) was the first to observe the expulsion of larvae by the polyps and described with some detail their settlements close to the mother colony (Faget & Vielzeuf 2018).

such as embryonic development and larval metamorphosis, have not yet been duplicated and verified. The studies cited above add new findings, mainly deriving from the application of new technologies not available 200 years ago (*e.g.,* videography and biochemical analyses). Consequently, some points developed by Lacaze-Duthiers require comment.

The first point concerns the sex of the colonies. Despite some studies on the subject having been performed, the presence of two sexes on the same colony has never been confirmed (Santangelo *et al*. 2003, Bramanti *et al*. 2009). However, it is difficult to reject the observations of Lacaze-Duthiers and this disagreement could have three origins: (1) in the population from North Africa studied by Lacaze-Duthiers, the red coral colonies would not have been gonochoric, but this seems unlikely; (2) Lacaze-Duthiers might have made his observations too early in the year (April-June), when the oocytes and seminal reservoirs are still not fully mature. In that case, well-developed seminal reservoirs could have been confounded with less developed oocytes. It is not infrequent that in a given female, the level of maturation of oocytes is not the same for all the polyps. With limited optical capacities, such as a 19th century microscope, the confusion between a female polyp having immature oocytes and a male polyp seems possible; (3) this pseudo-hermaphrodism could result from the fusion of two individuals, one male, one female, a phenomenon called chimerism described in red coral (Giordano & Bramanti 2021).

As indicated above Lacaze-Duthiers noted that "*the work of the reproductive organs is done in the spring and summer…and in the winter the propagation of the species stops and rests*" (HLD, p. 128). This observation has been confirmed by Santangelo *et al*. (2003) who reported that the size of oocytes remains small and almost constant until February, while from March to July their size increases quickly. Lacaze-Duthiers estimated the duration of brooding (*i.e.,* the time between fertilization and larval release) to be one month. Knowing that seminal reservoirs are still present inside male colonies 2-3 weeks before larval release, and assuming that fertilization happens when seminal reservoirs are no longer found, and that larval release happens 2-3 weeks later (Santangelo *et al*. 2003), then we can consider that brooding lasts 2 to 3 weeks, not far from the 1-month duration estimated by Lacaze-Duthiers.

The description of larval development and release made by Lacaze-Duthiers is almost perfect. Today, video cameras mounted on microscopes allow recording what Lacaze-Duthiers described with impressive details 200 years ago (a recording of a larva release is attached as supplementary material, https://wwwphp.obs-banyuls.fr/Viemilieu/index.php/volume-72-2022/72-issue-3-4.html). According to Lacaze-Duthiers, the release of embryos takes place in a consistent and continuous way from the end of August until September 15, decreases in October and entirely stops in November and December. Today, some authors think that larval release ends at the end of September (Santangelo *et al*. 2003, Zelli *et al*. 2020). The observations of new recruits in October and November reported by Lacaze-Duthiers are probably due to the small size of the settled larvae. It is likely that what he observed in November is the result of a settlement that happened at the end of September. Another possibility is that colonies from Algeria release larvae over a longer period, possibly due to different environmental conditions (*e.g.,* higher temperatures). According to Vighi (1972) the birth of larvae occurs during the period late July-early October and the free-living period of the larva is short: it varies between 4 and 12 days.

As indicated above, Lacaze-Duthiers noted that the larvae tend to swim upward. Those observations have been confirmed by Weinberg (1979) and in a more recent study establishing that red coral larvae spend more than 80 % of their time swimming upward (Martinez-Quintana *et al*. 2015), which is higher than any other sympatric gorgonians having similar larvae (Guizien *et al*. 2020, Viladrich *et al*. 2022). In recent years, studies on larval settlement added interesting details to Lacaze-Duthiers' observations. For instance, it has been shown that *C. rubrum* larvae settle less frequently in presence of some crustose coralline algae species (Zelli *et al*. 2020) but they do settle and survive on plastic debris (Carugati *et al*. 2021a). In addition, larvae that settle next to each other can fuse together forming chimeric individuals (Giordano & Bramanti 2021).

One point that Lacaze-Duthiers could not address probably because of his study's time constraint, is the age of maturity of the coral. According to recent age estimates based on annual growth ring counts, the minimum age at the first reproduction for *C. rubrum* varies between 6 and 10 years (Torrents *et al*. 2005, Gallmetzer *et al*. 2010).

Summary concerning the reproductive cycle

1 – The coral is gonochoric (always or most of the time) and viviparous.

2 – Cases of chimerism are observed.

3 – The timing of the coral reproduction is as follows: oocytes start increasing their size in March; sperm is released by male colonies in mid-July; larvae exit the female polyps at the end of July until the beginning of October; the free-living period of the larva can reach 49 days in absence of predators (in aquarium tanks) but it is probably much shorter in natural conditions (12 days); the settlement of the larvae generally ends late in October.

4 – During its free-living period the shape of the larva changes.

5 – Sclerites appear in the newly settled individual two weeks after settlement.

6 – Only the first polyp in a colony is the result of sexual reproduction, whereas all others that follow (hundreds

of them in the oldest colonies) are clones resulting from asexual budding [blastogenesis].

SKELETON[13] FORMATION AND CORAL GROWTH

Lacaze-Duthiers' contribution

Researchers who have studied the anatomy of the Mediterranean red coral have since the 17th century observed two mineral structures: a central axis, supporting the colony (used in jewelry and referred to as the axis), and small grains made of the same material (magnesian calcite) contained in the coenenchyme of the coral: the sclerites (also called spicules). A common question in the study of the coral is related to the formation of its axis. Swammerdam (quoted in Boccone 1674) and Réaumur (1727) were among the first to propose that the axis was formed by simple aggregation of sclerites. In the recent literature, this hypothesis is often and incorrectly attributed to Lacaze-Duthiers. One can quote the following passage: "*the conclusion of Lacaze-Duthiers is that the calcareous skeleton of Corallium rubrum is composed of sclerites inseparably cemented to form a continuous and non-segmented axis*" (Bayer 1996). Many other authors have reported this hypothesis in identical terms (Weinberg 1976, Grillo *et al*. 1993, Allemand & Bénazet-Tambutté 1996, Bayer & Cairns 2003, Vielzeuf *et al*. 2008, Cuif *et al*. 2011, Debreuil *et al*. 2012). In reality, a thorough reading of Lacaze-Duthiers' work indicates that his conclusions on that matter are subtler (Faget & Vielzeuf 2018). To understand the structure of the red coral axis, Lacaze-Duthiers studied the first stages of development of a colony by combining (1) observations in aquaria (until the end of September) to follow the fertilization and larval development, and (2) observation of samples collected at sea to observe the early stages of development of the axis (after September). One of Lacaze-Duthiers' first pertinent observations concerns the attachment of the larva to the substratum*: "the polyp is fixed by its coenenchyme to the rock that supports it… The bottom of its cavity or base is separated from the foreign body* [substratum] *by a coenenchyme blade, itself limited below by a thin epidermal layer… No calcareous blade is ever encountered below the animal…"* (HLD, p. 184 and 185). This is an important observation that we will have the opportunity to verify later. Then Lacaze-Duthiers passes to the description of the proto-axis, noting that the complex shape of the proto-axis, often *"horseshoe-shaped, usually higher towards the middle"* (HLD, p. 184 and Fig. 111(i)) in pl. XIX), is made of "*nuclei of stony substance which, all bulged, remind us, by their shape, of an agglomeration of spicules. The first impression that one feels when seeing them is that they are formed of gathered and agglutinated sclerites*" (HLD, p. 183-184). Then Lacaze-Duthiers focused his observations on the branch tip of a mature coral colony, assuming that the dynamics observed in the proto-axis should also be observed in the growing tip of the branch (HLD, p. 186-187). He observed "*perfectly regular whole sclerites, fused by one of their sides*" (HLD, p. 188). Even though the agglomeration of sclerites at the tip of a branch was first observed by previous scientists (Boccone 1674, Réaumur 1727, Cavolini 1785), Lacaze-Duthiers first clearly stated that the branch tip formed of aggregated sclerites necessarily becomes the medullary zone in a mature branch. He thus explains the complex shape of this medullary zone which is always found in a coral branch and which differs from the peripheral zone made of more or less concentric rings. *"The irregular nucleus and variable shape of the center of the sections perpendicular to the stem* [*i.e.*, medullary zone] *is due to the first shape of the axis, or to the trigonal body which, surrounded by concentric layers, became the center of a stem that developed gradually regular and cylindrical"* (HLD, p. 188; Fig. 37(i) and (j) in pl. VIII). It is important to emphasize that from the outset Lacaze-Duthiers establishes a difference between apical and diametrical growth and considers that "*the* [radial] *growth of the stem results from the deposition of concentric layers regularly molded on top of each other*" (HLD, p. 112). Another important passage contains the same idea: "*if we admit that the sclerites by their agglutination are added to the axis and contribute to its growth, we are forced to recognize that the axis is composed of two parts: one, the sclerites, coming from neighboring tissues; the other must be considered as a cement, it is deposited by the secretion which is carried out under the network of parallel canals… The cement is deposited in greater quantity on the body than at the ends of zoanthodemes* [branches]. *It is the cement that binds the nuclei of sclerites formed here and there in the coenenchyme*" (HLD, p. 122). All these points would be validated by subsequent work (Allemand & Grillo 1992, Allemand 1993, Grillo *et al*. 1993, Perrin *et al*. 2015).

Now, it is worth mentioning some Lacaze-Duthiers' conclusions that are partly incorrect. They concern the involvement of sclerites in the radial growth of the red coral axis, *i.e.*, in the annular zone as opposed to the medullary zone. In thin sections cut perpendicular to the axis of the skeleton (Fig. 4B, C), Lacaze-Duthiers observed colored radial bands, perpendicular to the growth rings (HLD, Fig. 37 in pl. VIII)[14]. He attributes the color of

[13] Skeleton and axis have the same meaning throughout the article.

[14] It is interesting to note that in his figure 37 Lacaze-Duthiers puts more emphasis on the radial structure with rays starting from the medullary part of the coral and bifurcations accommodating the increase in branch perimeter with age, than on the concentric rings of growth. He thus emphasizes the crystallographic structure of the coral that would be fully elucidat-

these radial bands to the incorporation of sclerites preferentially along the crests of the grooves (HLD, p. 189). Thus, for Lacaze-Duthiers, sclerites play a role in the radial (or diametrical) growth of the coral, even if this role is less important than at the apex, as noted above. He also reached this conclusion by cutting a thin section parallel to the axis of the branch, near the surface of the skeleton (HLD, Fig. 38 in pl. VIII). On those sections (which allow looking at the surface of the coral by transparency from the inside of the branch), Lacaze-Duthiers observes "*spiny packets*" (HLD, p. 189) which according to him are identical to sclerites. In this case, and in our interpretation, Lacaze-Duthiers probably confuses sclerites with the microprotuberances that punctuate the surface of the coral (for a picture of microprotuberances see Grillo *et al*. 1993, Vielzeuf *et al*. 2008, Perrin *et al*. 2015). The same misinterpretation has been made years later by Weinberg in his beautiful work on the sclerites of *Gorgonaceae* (Weinberg 1976, his plate 20).

It is surprising that Lacaze-Duthiers, who is usually meticulous in his observations, did not scrutinize the surface of the coral axis. In this case, his trained eye would surely have noticed the subtle difference between the morphology of the sclerites and that of the microprotuberances that cover the surface of the axis. Nevertheless, observing the tips of the branches Lacaze-Duthiers reported the presence of "*large nodules or packets of a darker red hue of a more or less spheroidal shape… These nodules have the surface completely covered with spinules, points or roughness*" (HLD, p. 121). He thus separates "spinules" (*i.e.,* microprotuberances) from "nodules" which most probably correspond to aggregates of sclerites covered with layers of calcite bristled with microprotuberances (Perrin *et al*. 2015).

The presence of sclerites in the annular zone of the axis postulated by Lacaze-Duthiers was questioned by Dantan (1928) who, without a formal demonstration, considered that "*if it is possible indeed that the central region is produced, almost always, by the agglomeration of sclerites, in the remainder of the axis the limestone has, probably, been directly secreted in the lamellar form that the preparations show*". This hypothesis and especially the fact that the growth of the annular zone does not involve sclerites have been demonstrated by Allemand and Grillo (1992) based on experiments of kinetics of calcium uptake and incorporation into the axial skeleton and sclerites. Those studies suggest that there is no delay between the calcification of the sclerites and the annular skeleton, which should be the case if the skeleton resulted from the aggregation of sclerites (Allemand & Grillo 1992; Allemand, 1993). While sclerites have *de facto* been observed in branch tips for centuries, their observation in the medullary zone of the axis, within an adult coral branch, as suggested by Lacaze-Duthiers, is only recent. Debreuil *et al*. (2011a) identified these sclerites by immune-staining of organic matter in the medullary zones of red coral. Subsequently, Perrin *et al*. (2015) unambiguously identified sclerites in the medullary zone, with scanning electron microscope and electron microprobe, based on their differences of magnesium and sulfur concentrations with respect to the surrounding calcitic cement[15]. Using this method of identification, Perrin *et al*. also identified some rare sclerites in the annular zone, without any particular arrangement.

Current state of knowledge

For technical reasons, Lacaze-Duthiers was unable to study the initial stage of skeletal formation immediately after the larva has attached to its substratum. Present-day studies of new recruits of known age in the aquarium carried out at Banyuls-sur-Mer show that the first (primary) polyp and those developing immediately afterward adhere organically to the substratum (as noted by Lacaze-Duthiers) and are protected by hundreds of sclerites that provide an effective shield when the polyp retracts (Giordano *et al*. 2022, see also our Fig. 3). The stage involving only sclerites and no axis lasts from a few months to just under two years. In two-year-old recruits, the onset of skeletal induration and cementing of the sclerites (formation of a medullary proto-zone) is observed, corresponding to the structures described by Lacaze-Duthiers (HLD, Figs 109 and 111 in pl. XIX). Note that a layer of calcitic cement has formed below the polyp(s) and from this point onwards, the recruit is firmly anchored to its substratum, and thus less sensitive to dislodgment and predation. The formation of an annular zone in the axis starts after 4 years of age (Giordano *et al*. 2022).

Other works on red coral skeletogenesis confirmed many of the points noted above by Lacaze-Duthiers. The growth of the tip of a branch does indeed involve the aggregation of sclerites, a mechanism that has been described as "block by block"[16] by Perrin *et al*. (2015). The same authors confirmed another observation by

ed much later (Vielzeuf *et al*. 2010). In contrast, the concentric growth rings (not visible in HLD's Fig. 37bis) are related to variations in chemical composition (see below). In a way, in the red coral's axis, a chemical structuring is concomitant with a crystallographic structuring. Different analytical techniques are required to characterize each type of structure, and a section of coral may show quite different features depending on the technique that is used.

[15] Note that the word 'cement' is used in the structural sense of a material (made of nanocrystals of MgCalcite) holding together separately built units (the sclerites, also made of nanocrystals of MgCalcite).

[16] The 'block-by-block' denomination might suggest a compact piling of sclerites with a small proportion of cement between them; this is not the case because the proportion of cement in the medullary zone is high compared to the proportion of sclerites (see Perrin *et al*. 2015, their fig. 4). The denomination of 'block and cement' is as appropriate.

Fig. 3. – Photograph of a 2-month-old red coral new recruit born in an aquarium at Banyuls-sur-Mer. Note the numerous sclerites inside the polyp. Compare to HLD, pl. II, fig. 7 (Photograph: L. Bramanti).

Lacaze-Duthiers, which was forgotten in the post-1864 models: Lacaze-Duthiers observed that before 'welding' to the skeleton, the sclerites often form aggregates that are cemented together and surrounded with calcite, forming independent blocks (possibly covered with microprotuberances) that progressively 'weld' to each other and then to the tip of the skeleton. This progressive formation of the skeleton at the tip could explain a singularity of the red coral reported by fishermen, recorded by Lacaze-Duthiers and long misunderstood, namely that *"sometimes elongated stems of coral are fished, up to a decimeter high, and whose skeletal axis is so small that one could suppose that it does not exist. In them, everything is, so to speak, bark (coenenchyme), so rapid has been the activity of budding (polyp development)"* (HLD, p. 66).

Perrin *et al*. (2015) generalized the "block-by-block" mode of growth at the branch tips to all species of the genus *Corallium*, in particular to two species (*C. johnsoni* & *C. japonicum*) for which it was accepted that the sclerites do not participate in skeletal growth. For example, for *C. johnsoni*, Lawniczak (1987) noted "*it seems impossible to retain any longer the theory of Lacaze-Duthiers (1864) according to which elements originating from the cortical tissues would migrate and fuse to the core of the branch by additional calcareous cementing*". For *C. japonicum* (or *Paracorallium japonicum*), Bayer & Cairns (2003) wrote that *"it is likely that sclerites have an insignificant or even non-existent role in the formation of the axis of Paracorallium"*. Thus, as already stated, for Lacaze-Duthiers, the radial growth of the axis is due to the "*deposition of concentric layers regularly molded on top of each other*" (HLD, p. 112) and "*deposited by the secretion that takes place under the network of parallel canals*" (HLD, p. 122). Instrumentation and methods at Lacaze-Duthiers' disposal did not allow him to identify an epithelial layer responsible for the formation of the axis between the axial skeleton and the parallel canals. This layer, studied by Grillo *et al*. (1993), comprises a single type of cells forming a layer of alternating thick (7 µm) and thin (less than 1 µm) zones. Regarding the annular domain and radial growth, Perrin *et al*. (2015) confirmed the previous conclusions that the growth mode was essentially "layer by layer". As indicated above, Perrin *et al*. also noted that rare isolated sclerites were present, although less abundant than Lacaze-Duthiers thought. These incorporations may seem anecdotal, but sclerites or groups of sclerites, incorporated on the surface of the subapical axis could represent nuclei to initiate secondary branches, or allow restart of growth on a broken branch (see HLD, Fig. 29, P, in pl. VII). Such secondary branches have been observed in colonies whose growth has been followed over long periods (J. Garrabou, pers. comm.).

The duality of "block by block" and "layer by layer" mechanisms raises two types of questions, on 1) the speed of growth of the colonies, which Lacaze-Duthiers acknowledges not having determined (HLD, p. 201)[17], and 2) the mechanism of shift between the two growth modes:

– The diametrical growth rate of the coral was estimated to be around 0.1 to 0.4 mm per year using two methods: 1) by following colonies over periods of several years (Garrabou & Harmelin 2002, Bramanti *et al*. 2005) and 2) by counting and measuring the width of growth rings (Marschal *et al*. 2004, Vielzeuf *et al*. 2008, Priori *et al*. 2013, Bramanti *et al*. 2014) that were determined to be annual (Marschal *et al*. 2004). The axial growth is about ten times faster and was estimated to be about 1.8 ± 0.7 mm per year (Garrabou & Harmelin 2002).

– The transition from one mode of growth to the other calls to mind an essential observation of Lacaze-Duthiers who noted the existence of two distinct but interconnected types of circulatory canal network in the tissues of red coral: a superficial network made of small, intertwined canals, and a deep network with larger canals (~0.2 mm) lodged in the coral grooves, at the axial skeleton surface

[17] Lacaze-Duthiers regretted not being able to determine the speed of coral growth. However, he indicated that he threw jars into the sea to begin an experiment on the duration of coral growth. (HLD, p. XXV). Nobody knows what became of these jars. A similar type of experiment (coral growth on tiles) would be carried out successfully 150 years later.

(HLD, pl. IV). The superficial network is present everywhere (at the tip and along the branches) while the deep network is present only along the branches where grooves in the axis are observed. This observation suggests that the deep network may act as a barrier between the area where sclerites are formed and the axis, preventing the incorporation of sclerites at the skeleton surface (Perrin *et al*. 2015). The change in skeletal growth mode would therefore be controlled by the anatomy and physiology of the organism and specifically by the presence of the deep canal network (Perrin *et al*. 2015). It is interesting that Lacaze-Duthiers had invoked this role of shielding by the deep canal network but with different implications. According to Lacaze-Duthiers, the canals placed in the grooves would prevent the aggregation of sclerites at this precise location. Conversely, between two canals, *i.e*., along the crests of the grooves, the sclerites would be more directly in contact with the skeleton. According to Lacaze-Duthiers, the incorporation of sclerites would take place at the level of these ridges (HLD, p. 189). We have seen above that this hypothesis has not been validated by recent observations (Grillo *et al*. 1993; Perrin *et al*. 2015). Nevertheless, the role of screen played by the deep canal network had been well suspected by Lacaze-Duthiers.

Interestingly, the study of the biomineral axis can provide indirect information on the biological functioning of the coral, *e.g*., affording an indication of the life span of a polyp. Indeed, below the polyps, the axis is smooth and does not show the crenulations that usually mark the surface of the axis. This is a fact that Lacaze-Duthiers had already observed*: "the bottom (of the cavities that contain the polyps) is smooth and does not offer striations like the rest of the stem… we are obliged to recognize that below the polyps, there are no vessels"* (HLD, p. 107; Fig. 114 in pl. XX). We thus have a marker for the presence either of canals or polyps. Vielzeuf *et al*. (2008) looked for this type of polyp marker inside coral skeleton sections and considered that the lack of crenulations at some locations along the growth rings indicates the presence there, at the time, of a polyp, there; the number of non-crenulated growth rings gives the polyp age. With this method, Vielzeuf *et al*. estimated the lifespan of a polyp to be 6 to 8 years. Using the same method on many coral sections, Benedetti *et al*. (2020) estimated the median age and the maximum life span of polyps to be 4 and 12 years, respectively, in agreement with the previous estimate.

According to Lacaze-Duthiers, the crenulated surface morphology of a branch in the sub-apical zone is related to the shape and arrangement of the deep canals, while the complex morphology of a branch tip is associated with the presence of numerous polyps. This observation implies an influence of the anatomy on the morphology of the skeleton. Following the same reasoning, Vielzeuf *et al*. (2017) suggested that the microprotuberances on the surface of octocoral skeletons could be linked to (and thus indicative of) the presence of cells or vacuoles that would

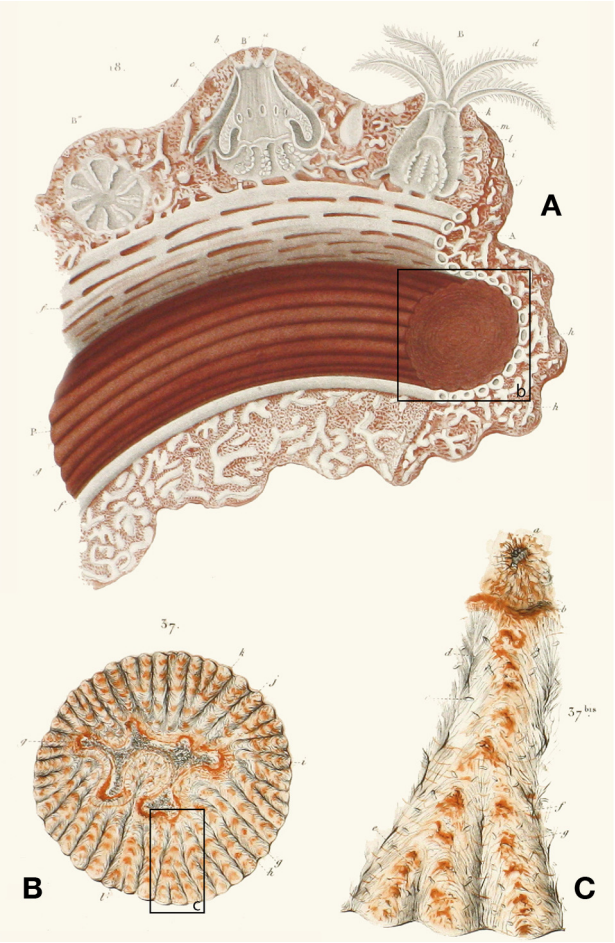

Fig. 4. – **A**: Extract from Lacaze-Duthiers plate IV showing the structure of the tissues surrounding the skeleton, and the organized network of deep canals. **B**: Section of skeleton perpendicular to the axis of the branch seen in thin section. A medullary zone is observed, different from the annular zone surrounding it. **C**: Enlargement of B. (Extract from pl. VIII). For Lacaze-Duthiers, the colored rays are due to the presence of sclerites, which turned out to be an erroneous hypothesis. Reprinted with permission from Faget & Vielzeuf (2018).

be part of an epithelium[18]. Along the entire branch, and at different scales, the morphology would then be dictated by the anatomy of the organism. Similar speculations were already present in the work of Lacaze-Duthiers who "*admits that the grooves are the consequence of the presence of the canals* (HLD, p. 107) and who speaks of the capacity of the canals "*to imprint their shape on the part on which they rest*" (HLD, p. 103)[19]. The notion of a mold provided by anatomical structures developed by Lacaze-

[18] A consequence of this spatial arrangement is that microprotuberances probably play an important role in the attachment of the coenenchyme to the axis.

[19] In spite of similarities, and as seen above Lacaze-Duthiers seems to think that the axis 'solidifies' and 'retain the imprint of the canals' (HLD, p. 78). Vielzeuf *et al*. (2017) do not think that the axis 'solidifies' but instead that it crystallizes in confined environments whose shapes are determined by the anatomical structures (polyps, canals, cells or groups of cells).

Duthiers may seem naive. In fact, it could be a remarkable phenomenological intuition since the idea of the confinement of crystalline deposits in organized tissues agrees with the theory on growth and shape of biominerals developed by Mann (1993), who considers that biomineral forms could be casts of an organic matrix which would have functioned as a mold.

In the same line of thought, and as a further illustration of the author's way of reasoning, it is interesting to note that looking at newly settled recruits Lacaze-Duthiers wonders "*how a circular blade almost entirely surrounding the animal* [the first polyp] [see HLD, Fig. 111 in pl. XIX] *can be transformed into a cylindrical axis which later will be placed within the tissues* [in the sense of becoming the medullary zone in the center of the axis]" (HLD, p. 190). This is an interesting question to which Lacaze-Duthiers provides an original answer: *"The first oozooid* [polyp]*, which is the true founder of a colony, produces a blastozooid* [secondary polyp born by budding] *which soon becomes as large as the first one; there are then two animals leaning exactly against each other, since they are equally developed* [Fig. 100 in pl. XVIII]. *The result is that the polypier* [here: nascent skeleton] *of the second will … oppose the convexity of its curve to the convexity of that of the first; from there is born a body necessarily with several angles… the blastozooids, by multiplying, add new solid elements to the small primitive mass."* (HLD, p. 190). It follows that the position of the polyps on the colony affects the shape of the axis. Based on a similar idea, Perrin *et al*. (2015) considered that the position of the polyps at the tip of the branch triggers and determines the branching of the colony (and also the shape of the colony as a function of its environment). What biological mechanisms trigger the development of a new polyp (and prevent the development of others) remains an exciting research direction to explore.

Summary concerning the skeleton formation and coral growth

1 – At the outset of its settlement, the larva adheres to the substratum in an organic way.

2 – During the first months of their life (up to almost two years), the first polyp and those which follow by budding are protected by sclerites which form an effective, deformable and extensible mineral shield when the polyps fold.

3 – After two years, the cementation of the sclerites begins and the skeleton is mineralogically anchored to the substratum. The coral initiates the formation of the skeleton by forming what will become a medullary zone of the axis by a "block-by-block" (or "block and cement") process.

4 – The formation of an annular zone starts later (after 4 or 5 years). The coral then enters an immature phase, which will last until the sexual maturity of the colony (at the age of 10 to 15 years). Following this period, the coral enters its adult phase, which will last a few decades (up to a hundred years; older colonies probably exist but information is lacking on this subject)[20].

5 – The polyps are builder animals (an apt metaphor long applied to diverse corals) that join their capacities to produce sclerites and cement essential in elaborating the solid axis of the skeleton. The form of the skeleton depends among other things on the hydrodynamic conditions; the axis morphology plays a role in optimizing the capture of food, allowing the proliferation and maintenance of the colony.

SCLERITES[21] (OR SPICULES)

Lacaze-Duthiers's contribution

Lacaze-Duthiers gives an important place to sclerites, structures described as early as the 17th century by Swammerdam (HLD, p. 123-124). Valenciennes (1855) introduced the term 'sclerites' and was the first to use sclerite morphology to identify groups and species of octocorals (Bayer *et al*. 1983). Lacaze-Duthiers provides a precise description of red coral sclerites both in the text and in his plates (*e.g*., HLD pls IV, VI). He gives an exact determination of their size: "*The dimensions of the sclerites do not exceed certain limits; the largest measure 5 to 7 hundredths of a millimeter* [50 to 70 µm]*, rarely more. But they are infinitely smaller in the first moments of their formation* [HLD, Figs 24 to 26 in pl. VI]. *It is only gradually that they reach their usual size"* (HLD, p. 74). Lacaze-Duthiers pays particular attention to the change in size and shape of the sclerites: "*…the sclerites begin as small, almost cylindrical rods, obtuse and rounded at both ends* (HLD, Fig. 92c in pl. XVI) *… they measure … twice as long as the diameter of the cells of the tissue… (These sclerites are one and a half hundredth of a millimeter long* [15 µm] *and half a hundredth* [5 µm] *wide)…; they are not colored and they refract light in much the same way as the parts which surround them…; When their ends cease to be obtuse, they become triangular* (HLD, Fig. 92d in pl. XVI)… *The secondary rough edges* [or bulges] (HLD, Fig. 92 h, i, in pl. XVI) *gradually develop, but hardly occur all at once; they are also less regular in the tissue of the oozooid* [polyp] *than in the coenenchyme of a well-developed zoanthodeme… It has already been seen that when the spicules were not very complete, they represented two isosceles triangles superimposed base to apex* (HLD, Fig. 26 in pl. VI). *This arrangement seems,*

[20] Some colonies of large size (such as those in Natural History Museums or used in sculpture) have not been chronologically aged but are much larger than scientifically dated colonies approaching 100 years old, which suggests ages greater than 100 years.

[21] Lacaze-Duthiers always uses the term 'spicule'.

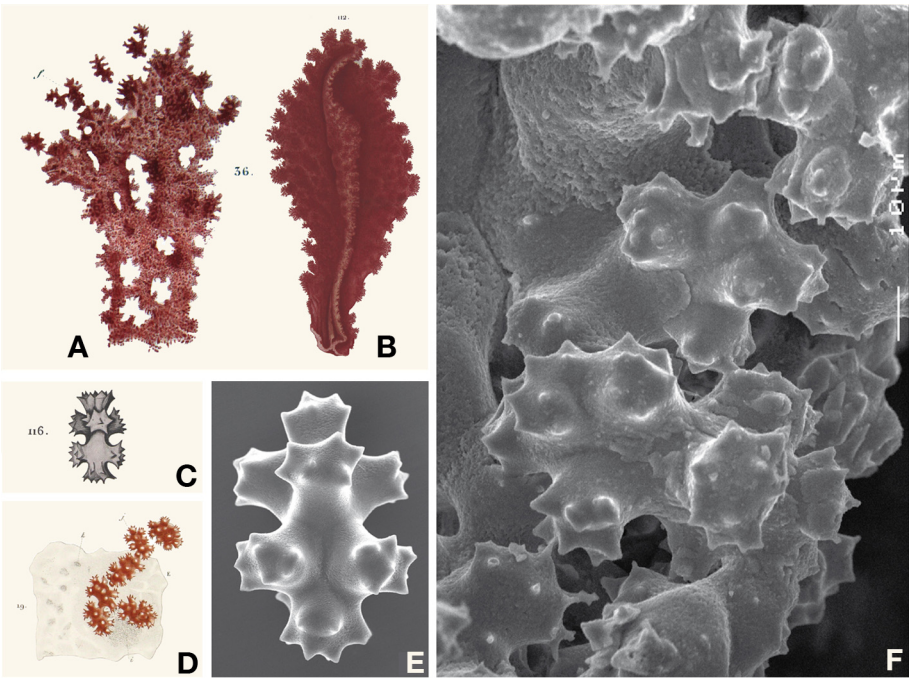

Fig. 5. – **A**: Extract from plate VIII of Lacaze-Duthiers showing the tip of an axis in the process of formation. **B**: Extract from plate XX of Lacaze-Duthiers showing the skeleton at the end of a branch (branch drawn alive in our Fig. 2A). These tips are made of aggregated sclerites. **C**: Extract from Plate XX of Lacaze-Duthiers showing a sclerite. **D**: Extract from plate IV of Lacaze-Duthiers showing the sclerites in the tissues. **E**: A sclerite observed with a scanning electron microscope (compare to C). **F**: Scanning electron microscope image showing the aggregated and cemented sclerites in the branch tip. Reprinted with permission from Faget & Vielzeuf (2018).

in the development, always to precede the final form". (HLD, p. 179, see also p. 71).

Equally important, Lacaze-Duthiers discusses the position of the sclerites within the coral tissues (HLD, Fig. 18 in pl. IV) including polyps (HLD, Fig. 7 in pl. II). These results were later confirmed by Grillo *et al.* (1993), although these authors rarely observed sclerites in polyps. Throughout his text, Lacaze-Duthiers notes the importance of the number eight in the organization of the organs in red coral, which is consistent with their taxonomic placement in what would be called the Octocorallia (Haeckel 1866) soon after Lacaze-Duthiers' book was published. Concerning the sclerites, Lacaze-Duthiers also notes that most of the time, the sclerites have eight tubercles (or bulges); but he also notes, and this time erroneously, that the tubercles end in *'eight rows of spines*' (HLD, Fig. 25 in pl. VI).

Concerning the formation of the sclerites, Lacaze-Duthiers wrote: "*In spite of all the efforts and all the care of preparation, it was impossible for me to be sure if these elements developed in the interior of a cell. The thing seems probable, for in many Alcyonaria* [now known as Octocorallia] *they are so large and so isolated, that, in a thin section of the tissue, it is easy to have only one of them in the field of the microscope, and one can then distinguish a double outline which perhaps indicates an envelope. It is, however, very difficult to affirm when such delicate things are involved; and it must not be forgotten that, in the Alcyons in particular, the general tissue or coenenchyme is almost cartilaginous, and that the space, the cavity in which the sclerite is housed, may, in itself, produce this appearance*" (HLD, p. 178). New developments on that matter are discussed below. It is important to emphasize here that according to Lacaze-Duthiers, "*sclerites are not accidental deposits. They are parts secreted by the organism… and it is impossible to exclude them from direct vital action. The sclerites have as much reason to belong to the being itself as the rest of the body"* (HLD, p. 192).

Current state of knowledge

Concerning the morphology of sclerites, it is now known that they have different shapes (cross or dumbbell), although the more common is the dumbbell shape described by Lacaze-Duthiers. In this case, a sclerite consists of an elongated central body and eight tubercles, two as an extension along the long axis of the sclerite and six laterally arranged in two groups of three tubercles, with a rotation of 60° between the two groups (Fig. 5E). It should be noted that Lacaze-Duthiers did not capture the systematic character of the 60° rotation between the two lateral groups: in some figures the sclerites are correctly represented (HLD, Figs 24b, 116 in pls VI, XX) while in others they are erroneously pictured (HLD, Figs 19 and 24a in pls IV, VI). This is probably because Lacaze-Duthiers observed the sclerites in transmitted light and that a tubercle below the sclerite can easily appear as placed above. It is now known that sclerites comprise an assembly of small crystals of magnesian calcite of about 80 nm, crystallographically oriented in an almost identical way, but with slight misorientations in three directions related to the crystalline symmetry and crystallographic axes of the calcite (Floquet & Vielzeuf 2011, 2012). The configuration of the tubercles is a direct consequence of the crystalline organization of the sclerite, and it is not the number

eight that best characterizes the organization of sclerites (as suggested by Lacaze-Duthiers), but rather the number three. However, Lacaze-Duthiers' geometrical intuition to represent nascent sclerites as two superimposed isosceles triangles (HLD, Fig. 26b in pl. VI) was particularly interesting. A more accurate three-dimensional image would be the imbrication of two triangular-based pyramids with 60° rotation between them.

In terms of formation of sclerites, it will be noted that a few years after the publication of the *Histoire naturelle du corail*, von Koch (1882) suggested that the spicules of *Clavularia prolifera* form within a cell that is shed from the ectoderm. The fine work of Kingsley and Watabe in the 1980s described the initial intracellular formation of the spicules in the gorgonian *Leptogorgia virgulata* and their release into the mesoglea where they complete their growth (see Kingsley 1984 and Watabe & Kingsley 1992 for reviews). A similar description was made on red coral by Grillo *et al*. (1993). Later, Le Goff *et al*. (2017) showed by immunofluorescence that the growing sclerites are enclosed in two cells[22]. Thus, in the red coral, as in other Octocorallia, after a transient intracellular step, sclerite growth occurs by an extracellular process controlled by at least two cells joined by septate junctions before the release of the mature sclerite into the mesoglea (see for review Conci *et al*. 2021).

Now we will address the question of the functions of the sclerites in the red coral. In the case of new recruits, as seen earlier the role of sclerites as elements of an assembly forming an efficient, deformable and easily expandable armor protecting the fast-growing primary and early polyps is likely (Giordano *et al*. 2022). Thus, sclerites play a major role in protecting newborn corals (Fig. 3), which is critical for their survival. Concerning adult colonies, the role of sclerites is more debated. In her review, Kingsley (1984) suggests various functions for sclerites in marine invertebrates such as: 1) protection against predators; 2) structural integrity/support; 3) enhancing stability within the substratum; 4) anchoring during locomotion; 5) sensory function for transmission of tactile stimuli; 6) mechanical protection against abrasion; 7) detoxification system for controlling dangerous levels of calcium ions in the cells. As far as the red coral is concerned, Allemand (1993) noted that sclerites are often found on the bottom of the aquarium in which the red coral grows, suggesting that they are eliminated from the organism. This important observation is consistent with the fact that sclerites have a high production rate of about 10 sclerites synthesized per day and per mg of coral protein (Allemand & Grillo 1992), so they need to be permanently removed from the tissues. Nevertheless, and as noted above, some of these are incorporated into the medullary zone of the axis, so this function was possibly acquired by a process of exaptation as it is not observed in other octocorals that do not build a hard skeleton. Furthermore, from Lacaze-Duthiers and other structural studies (Perrin *et al*. 2015) it is possible to consider that sclerites serve as crystalline nuclei (formed intracellularly at their initial stage) facilitating the initiation of the extracellular formation of calcites around them. In addition, and as suggested by Lacaze-Duthiers, the position of the polyps in the colony can be seen as a factor contributing to the spatial arrangement of sclerites and thus blueprinting the shape of the colony. In this respect the shape of the medullary zone, its position at the core of the axis, the timing and initiation of branching, could be the result of the arrangement of sclerites directly following the spatial arrangement of the polyps (Perrin *et al*. 2015).

[22] As indicated earlier, Lacaze-Duthiers noted that the sclerites begin as small rods, twice as long as the diameter of the cells of the tissue.

Summary concerning the sclerites

1 – Sclerites are small grains of magnesian calcite in the living tissues of the red coral.

2 – Most of the time, sclerites display a characteristic dumbbell shape with an opposite (with respect to a center of symmetry) arrangement of eight tubercles.

3 – Sclerites are made of ca. 80 nm similarly-oriented magnesian calcite crystals. A small degree of misorientation is observed between them, but these misorientations are not random: they happen along particular crystallographic axes of calcite. The shape of the sclerites is related to the crystallographic properties of calcite. The morphology and crystallography of the sclerite are connected, and in many cases, the sclerite morphology can be indicative of the internal crystallographic organization of the sclerite.

4 – Sclerites participate in the construction of the medullary zone in the axis (via a block-by-block (or block-and-cement) growth mode). They are much less common in the annular zone (layer-by-layer growth mode).

5 – Sclerites play a major role protecting the first-settled polyps from predation.

6 – Sclerites serve as nuclei for further biomineral deposits and probably play a role in the adjustment of the shape of the colony for better adaptation to hydrodynamic conditions.

7 – Sclerite production rate is high, and they are regularly expelled by the coral.

CHEMICAL COMPOSITION OF THE SKELETON AND ORIGIN OF COLOR

Lacaze-Duthiers' contribution and comments

Lacaze-Duthiers devoted a short chapter (p. 214-219) to the chemical composition of the red coral skeleton. He quotes the only consequential determination published up

to that time by Vogel (1814)[23]: Carbonic acid (H_2CO_3)[24], 27.50 wt %; Lime (CaO), 50.50; Magnesia (MgO), 3.00; Iron oxide (FeO), 1.00; Water (H_20), 5.00; Animal debris (organic matter?), 0.50; Lime sulphate ($CaSO_4$), 0.50; Sodium muriate (NaCl), trace. So, according to this analysis, the axis would contain the following elements: H, C, O, Ca, Mg, Fe, S, Na, and Cl. This is a remarkable result because (1) these elements are indeed present in the axis (with iron and chlorine in very small quantities)[25], and (2) the presence and importance of certain elements such as sulfur and sodium, though is low concentrations, has been emphasized recently (Vielzeuf *et al*. 2018). In terms of concentration, 50.5 wt% CaO and 3.00 wt % MgO correspond to 360920 µg/g (or ppm) calcium and 18096 µg/g magnesium respectively. This is again a remarkable result when compared to the most recent values obtained on coral axes using modern analytical techniques: Ca: 340000 to 360000 µg/g; Mg: 23000 to 32000 µg/g. We note that Vogel's analysis underestimates the magnesium content, probably due to the means available to chemists at that time. The conclusion that coral is a '*carbonate of lime*' would have been perfect if Lacaze-Duthiers had also pointed out the presence of '*carbonate of magnesia*', which he did not.

Concerning the current analyses, we note a relatively large range of calcium and magnesium contents. This is due to an intercolonial variability of composition, but also to relatively large intracolonial variability (*i.e.,* within the axis of a coral branch). Indeed, the magnesian calcite chemical composition differs between (1) growth rings, (2) cement in the medullary zone, and (3) sclerites. On the other hand, in the annular zone (or growth ring zone), a variability in chemical composition also exists within each growth ring. Vielzeuf *et al*. (2018) relate the magnesium-rich parts of these rings to rapid skeletal growth occurring during the summer period, while the Mg-poor (and therefore calcium-rich) parts would result from slow growth during the winter period.

As for the chemical composition of the sclerites, Weinbauer *et al*. (2000) noted that the sclerites are richer in magnesium than the axis. A more recent work confirms this observation and notes that *C. rubrum* sclerites are richer in Mg and Rare-Earth Elements, and poorer in Ca, Sr, Na, and S, than the axis (Vielzeuf *et al*. 2018). In addition, the axis and sclerites display two distinct but positive Sr/Mg correlations and the concentration in organic matter is higher in sclerites than in the axis (Allemand *et al*. 1994, Perrin *et al*. 2017, Vielzeuf *et al*. 2018). For instance, Allemand *et al*. (1994) found that organic fraction represents about 1.1 % to 1.6 % of the total weight of the axial skeleton and sclerites, respectively.

Interestingly, variations of compositions occur inside the sclerites, which allows the identification of growth rings. Three to five growth rings are commonly identified inside sclerites (Giordano *et al*. 2022) together with secondary, less marked growth rings. Sclerites develop fast, as they are fully developed in 17-day-old recruits (Giordano *et al*. 2022), thus it seems likely that well-marked growth rings correspond to diurnal cycle, which may indicate that sclerites reach their mature size and morphology in about 3 to 5 days.

Returning to Lacaze-Duthiers, he concludes from Vogel's analysis that *"[red] coral is a carbonate of lime mixed with very small proportions of organic products"* (HLD, p. 214). For Lacaze-Duthiers, these "organic products" were animal debris. It is interesting to note that the presence of organic matter specifically secreted by the animal has been the subject of intense debates between biologists and geochemists, for both Octocorallia and reef-building corals (Hexacorallia: Scleractinia). Indeed, until the 1960s the idea prevailed that skeletal formation was the result of purely mineralogical processes (Hyman 1940, Bryan & Hill 1941). The demonstration of the presence of an organic matrix dates from the 1990s using both histological and biochemical methods (Grillo *et al*. 1993, Allemand *et al*. 1994). The red coral organic matrix has since been the subject of numerous studies (Debreuil *et al*. 2011a, b, 2012, Le Goff *et al*. 2016, Le Roy *et al*. 2021).

More than the chemical composition, what interests Lacaze-Duthiers is the *"nature of the coloring matter"* (HLD, p. 214) of the axial skeleton. For Vogel, the red color is not due to the presence of 'animal' (*i.e.,* organic) matter but to iron oxide, an idea that can still be found in the 20th century (Ranson & Durivault 1937). However, Lacaze-Duthiers notes that not all chemists share this opinion and reports an interview with G. Fremy (Professor of Chemistry at the Muséum National d'Histoire Naturelle in Paris) who considers that *"the color is perhaps of the same nature as that of the shells… which is obviously an animal matter"* (HLD, p. 215).

The problem of the nature of the coloring matter of the coral would be solved in the early 1980s through the development of Raman spectrometry. Merlin & Delé-Dubois (1986) demonstrated that polyene chains are at the origin of the color of many marine organisms, including red coral. Polyenes are polyunsaturated organic compounds that contain at least three alternating double and single carbon-carbon bonds. The carbon-carbon double bonds interact in a process known as conjugation resulting in unusual optical properties.

Merlin & Delé-Dubois (1986) showed that there is a linear relationship between the wave number $\upsilon 1$ (related to the vibration mode of the C=C double bond in polyene chains (C=C stretching frequency)) and $\upsilon 2$ (characteristic of the vibration of the single bond C-C stretch-

[23] This analysis is probably one of the oldest chemical analyses of biomineral ever published.

[24] The chemical formulas in brackets have been added by us.

[25] Iron and chlorine concentrations are < 1 µg/g, < 300 µg/g, respectively (Vielzeuf *et al*. 2018, Ricolleau *et al*. 2019) undetectable by the technical means of HLD's time.

ing mode) in marine skeletons colored by polyenic molecules. Another type of linear correlation between $\upsilon 1$ and $\upsilon 2$ exists for polyene chains of the 'carotenoid' type. But the two correlations do not overlap and Merlin and Delé-Dubois explain the differences by the influence of lateral methyl groups (CH_3) on the vibrational modes of carotenoids. The $\upsilon 1$ vs $\upsilon 2$ diagram is thus an efficient tool to distinguish unmethylated pigments from methylated carotenoid pigments (such as beta-carotene or canthaxanthin (4,4'-diketo-beta-carotene)). The pigments of red coral would therefore be polyenic chains without methyl side groups (*e.g.,* unmethylated, or unsubstituted). Finally, there is a relationship between the chain length of the polyene and the value of the wave number $\upsilon 1$, the number of C=C double bonds (or C-C=C units) increases when $\upsilon 1$ decreases. According to this relationship, and still according to Merlin & Delé-Dubois, the pigment of red coral would contain 11+/-1 double bonds. Merlin & Delé-Dubois also note that "*In view of the possible diversity of polyenic chain environments in these calcareous skeletons it is probable that the color results not from a single factor but from the interplay of a number of effects, and polarization of the pi system, induced by charged groups. Concentration of the pigment and structural effects due to the nature of the skeleton can also be considered to explain the shade of the colors*" (Merlin & Delé-Dubois 1986, p. 102). The same authors also note that a complete understanding of the structure of these polyenic pigments would need careful extractions, purifications and chemical analyses followed by spectroscopic investigations.

This is what Cvejic *et al*. did in 2007, performing analyses on both soft (coenenchyme) and hard tissues (sclerites and axis). Since hard tissues are made of mineral and organic fractions, extraction of the pigments was performed both with and without demineralization. Cvejic *et al*. (2007) confirmed the presence of polyenic chains in natural samples of *C. rubrum* skeletons and concluded that canthaxanthin, 4,4'-diketo-*beta*-carotene, is the major pigment in both soft organic and hard tissues of the red coral. In addition, the authors noted that sclerites have higher contents of carotenoids than the axial skeleton. This is consistent with the higher percentage of organic matrix in sclerites than in skeleton (Allemand *et al*. 1994, Perrin *et al*. 2017, Vielzeuf *et al*. 2018).

In the same study, Cvejic *et al*. (2007) make additional observations: (1) both sclerites and axis are responsible for the red color of the coral, and (2) the compounds responsible for red color in the hard tissues are in such a structural context that they are not denaturated by slight heating and chemical treatment. They further note that the polyenic chain responsible for the red color can only be supplied through feeding on plankton containing polyenes since animals are not able to synthetize polyenes themselves. Finally, Cvejic *et al*. discuss the 'evolutionary' advantage of the presence of pigments in the tissues of the red coral. As in the case for other organisms, polyenes in *C. rubrum* might protect the tissues from reactive oxygen species (ROS) produced endogenously but the low aerobic metabolism of red coral (the respiratory rate of a red coral colony is as low as only 1.60 ± 0.43 [S.D.] micromol O_2 day^{-1} mg $protein^{-1}$, Allemand & Grillo 1992) does not really justify a need for such a high concentration of carotenoids. Nevertheless, the production and incorporation of the pigment into the axial skeleton and sclerites has a definite energetic cost and its maintenance during evolution must have required significant selective pressure, especially as albino *C. rubrum* colonies exist, but remain rare. In short, the role of polyenes in the axis and sclerites is yet to be determined.

Fritsh & Karampelas (2008) noted that the results from Cvejic *et al*.'s paper do not fully agree with Merlin and Delé-Dubois' conclusions. Even if both studies conclude that polyenic chains are responsible for the red color of the coral, they differ on the exact nature of the pigment (unsubstituted polyene for Merlin & Delé-Dubois, canthaxanthin (polyene with lateral methyl groups, *i.e.*, methylated) for Cvejic *et al*. 2007). In addition, using different excitation wavelengths on the Raman spectrometer, Fritsch & Karampelas (2008) observed that the position, shape and intensity of the u1 band (at about 1520 cm^{-1}) vary, demonstrating the presence of more than one component bands, each for a pigment having a given number of double bonds. Thus, the red color would not be due to a single pigment, but a mixture of pigments belonging to the same family but with the number of double bonds varying between 9 and 11. This is another factor that might explain variations in the color of red coral.

To reconcile the data of Merlin & Delé-Dubois with those of Cvejic *et al*. we may note that canthaxanthin is a polyene chain comprising a succession of 9 conjugated double bonds, a number close to that of unmethylated chains in red coral. As an explanation, we therefore suggest that unmethylated chains in fresh coral specimens could have been methylated during the extraction and chromatographic analysis processes performed by Cvejic *et al*. If this hypothesis were to prove true, it could mean that the side bonds of the polyene chains in coral are connected to the crystal lattice of calcite. Such a structural effect could also explain in part the color shades observed in red coral.

Some new results

A Raman image of a section of red coral skeleton cut perpendicular to its axis obtained with a Thermo Scientific DXR2xi Raman imaging microscope is shown in Fig. 6. The analyzed area is 2.65 mm × 1.80 mm and a 20× objective, with a confocal aperture of 50 µm, was used to collect the Raman data. The image pixel size is 5 microns giving an image based on 190,800 spectra. A 532 nm laser was used. The image is the result of a MCR (Multivariate Curve Resolution) analysis of the spectroscopic data.

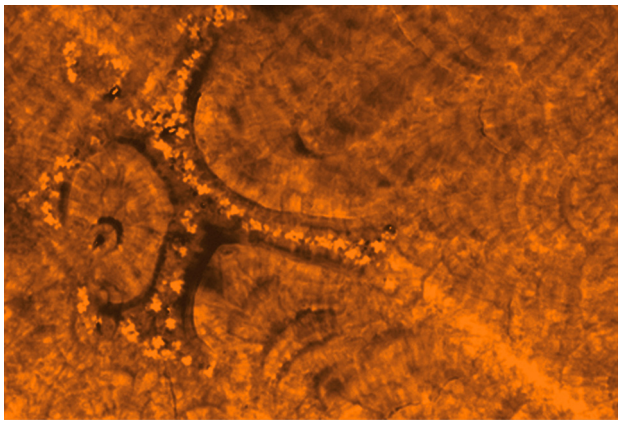

Fig. 6. – Raman image of a section of red coral cut perpendicular to its axis. The pigment content increases with brightness. Sclerites can be identified in the medullary zone.

MCR is a signal processing method that helps to differentiate the Raman spectra into components; the constituents are assigned different colors to produce a chemical image. In this case, the Raman spectra are a combination of only two signals: the inorganic component (magnesian calcite) and the pigment (polyene chain) which, despite its low concentration (<< 2 wt %), provides an intense Raman signal. In Fig. 6, the pigment is bright orange, calcite is grey, and the concentration of the pigment increases with perceived brightness.

On this image, the medullary zone is identified: it is made of (1) a cement that is in general poorer in pigments than the annular zone, and (2) sclerites that are much richer in pigments than both the medullary cement and the annular zone. With this method, sclerites can be easily identified in the medullary zone. In the annular zone, variations of pigment concentrations are also observed. They mark the growth rings but also the radial arrangement of crystallographic units that compose the skeleton (Vielzeuf *et al*. 2010). This Raman image compares remarkably with Lacaze-Duthiers' figures 37 and 37bis in his Plate VIII. It is also worth noting that Lacaze-Duthiers points out that sclerites are redder in adult colonies than in the new recruits. As indicated above, this is a point that has been checked by Cvejic *et al*. (2007). To conclude this section, we suggest that the distribution and concentration of the pigments are the main factors affecting the variations of color.

Summary concerning the composition and the color of the red coral

1 – The red coral axis comprises about 98 wt % magnesian calcite and 2 wt % organic matter.

2 – Elements composing the axis are (in decreasing order of contribution to mass) O, Ca, C, Mg, Na, S, Sr, H, (and minor amounts of K, P, B, Ba, Fe, Li, Mn, Pb, and U)

3 – Calcites from the sclerites, medullar cement and annular zone have slightly different composition, which some authors attribute to growth rate variations and growth mode. The growth rings marked by variations of compositions and concentration of organic matter might thus reflect variations of growth rate during the year.

4 – Calcites from the sclerites are richer in organic matter, pigments, and magnesium, and poorer in Ca, Sr, Na, and S than calcites from the axis.

5 – Polyenic chains (most likely unmethylated) are responsible for the red color of the axis. The concentration of pigments is higher in sclerites than in the medullary or annular zones

ECOLOGY AND PROPOSALS FOR SUSTAINABLE FISHING

Lacaze-Duthiers' observations and comments

In his work, Lacaze-Duthiers is concerned with the most favorable conditions for red coral development and notes that *"In winter, the vital resistance* [of the coral] *to the action of external agents is much greater* [than during the summer]… *It is from 12 to 15 degrees that the blossoming* [extension and expansion of the polyps] *is ordinarily most complete"* (HLD, p. 40-41). But he also notes that beyond certain temperatures, the coral does not survive: *"It is necessary to take great account of the temperature; it rose frequently, in the aquariums, to 20, 22 and 23 degrees. During the summers of 1861 and 1862, in spite of all imaginable care, it was impossible to keep coral for a long time: it died with a rapidity that could only be attributed to the heat or the season. On the contrary, observation in the months of September, October, November and December is very easy: a small branch fished on October 15 at Cape Rosa lived until the end of December of the same year"* (HLD, p. 40). This is again a remarkable observation since controlled experimental studies show that coral cannot tolerate temperatures of 24° or higher (Torrents *et al*. 2008). However, it should be noted that shallow population have higher tolerance to thermal stress than deep ones (Cau *et al*. 2018). The optimum temperature range for red coral proposed by Lacaze-Duthiers (12 to 15° C) has not been confirmed but studies on the bathymetrical distribution of the species in Sardinia showed that the higher abundance can be found between 100 and 200 meters (Carugati *et al*. 2021b) where the seawater temperature is almost constant at 13° C[26]. Anyway, as the spatial distribution of the red coral depends on many factors, the observation from Sardinia may not apply to other areas where red coral populations can be observed in shallow habitats (*e.g*., Garrabou & Harmelin

[26] 13° C is the lowest seawater temperature in the Mediterranean even at great depths.

2002, Garrabou *et al*. 2017). Lacaze-Duthiers notes in various places in his book *"the so rapid and consistent death of coral, even in the sea, during great heat"* (HLD, p. 156, see also p. 41). This is another notable observation as until recently it was thought that the phenomenon of mass mortality of benthic suspension feeders started at the end of the 1980s, with dramatic mass mortalities observed in the northwestern Mediterranean. One of the first well identified cases of red coral mass mortality was reported in 1983 between Marseille and La Ciotat (France) and possibly attributed to unusual hot seawater temperatures (GFCM 1984). This phenomenon was therefore already observed in the nineteenth century, and perhaps the question of the origin of such events, possibly linked to a combination of causes, should be reconsidered. According to Torrents *et al*. (2008) and Gómez-Gras *et al*. (2021) both the temperature and the time of exposure to a certain temperature play a role in the mortality of red coral colonies. However, mortality may not simply be due to a temperature effect but also to a bacterial infection (*Vibrio coralliilyticus*), as shown for *Paramuricea clavata* (red gorgonian), a conclusion that could be also valid for red coral (Bally & Garrabou 2007).

Based on his observations and discoveries, Lacaze-Duthiers discusses the problems of coral fishing in the last two parts of his book and suggests improvements. "*The mission with which I had the honor of being entrusted had as its main aim to find out whether the banks were not depleted by overactive and continuous fishing, whether it would not be possible to develop them in such a way as to increase the quantity and value of the products, and whether, in the knowledge of the facts relating to reproduction, it would not be possible to find suitable guides for regulating fishing in such a way as to obtain more satisfactory results in all respects*" (HLD, p. 266). Lacaze-Duthiers had also his precursors: nearly a century and a half earlier, Count Luigi Ferdinando Marsigli had likened the unrestrained harvesting of red coral populations to the clear-cutting of terrestrial forests and proposed the need for a decades-long pause in harvesting to allow renewal of the corals (Marsigli 1725).

Lacaze-Duthiers proposed a project of "*regulation… to draw the attention of the administration to a host of important issues in this industry*" (Lacaze-Duthiers 1862, p. 39). In particular, he suggested employing seasonal harvesting to avoid the coral's reproductive period (see section 'Historical context of Lacaze-Duthiers' study' above). This suggestion could represent one of the first examples of fishery regulation based on scientific information (Shick 2018, p. 180). Lacaze-Duthiers also suggested regulations to *"prohibit the use of iron machines* [meaning devices such as the St Andrew's cross], *dredges, and anything that can, by scraping the rocks* [such as the salabre], *destroy the young coral colonies*" (HLD, p. 322). However, these were not definitively banned in European waters until 1994. In recent decades, red coral harvesting by Mediterranean countries has been regulated not only by seasonal closures but also by quotas, number of boats and divers, depth restrictions, and size restrictions on colonies harvested (Bruckner 2016). It is worth noticing the modernity of Lacaze-Duthiers' proposal of regulating the fishery based on scientific data, something that is still advocated today, especially in red coral management and restoration (Santangelo *et al*. 2007, Bramanti *et al*. 2009, Tsounis *et al*. 2013, Cannas *et al*. 2014). In the last few years, management decisions on red coral fishery have been based on scientific data. For example, GFCM (General Fishery Commission for the Mediterranean) prohibited the use of remotely operated vehicles (ROV) for red coral fishery (GFCM 2010) and banned red coral fishery in the first 50 meters depth according to the advice of its scientific committee (GFCM 2011). Spain totally prohibited red coral fishery on the basis of a scientific report alerting regulators to the poor condition of the stocks due to overexploitation and mass mortality events linked to temperature increase (Garrabou *et al*. 2019).

Finally, in order to promote coral management, Lacaze-Duthiers proposed developing a kind of coral farming: *"It is difficult to deal with a fishing issue today without farming in mind"* (HLD, p. 277). Thus, he proposed a system for catching larvae: *"Bricks of a certain conformation, on which the larvae would settle, would be in good condition to be transported to well-chosen places in advance"* (HLD, p. 278). The same approach is behind the *in situ* coral culture experiments developed in Monaco in 1988 (Cattaneo-Vietti *et al*. 1992, Debernardi 1992, Allemand 1993, Allemand *et al*. 1995), in Italy (Bramanti *et al*. 2007, Villechanoux *et al*. 2022) and more recently in Banyuls-sur-Mer and Monaco in the framework of an ongoing project (Allemand & Bramanti pers. comm.).

CONCLUSION

Scientific ethics require that previous work on a subject under investigation be cited. But the most important things for the progress of science and the satisfaction of present-day researchers are (1) not to rediscover (or recast) something that has already been discovered, and (2) to build their research on results already obtained for faster and more efficient advancement. Indeed, "*standing on the shoulders of giants*" is a metaphor expressing that the new discoveries in science are often achieved by building on those made by earlier researchers. However, this previous research must be accessible to all, although in the case of Lacaze-Duthiers' monograph on red coral, which is available on the web, it is the lack of an English translation that may hinder its informed citation. Further, both the exponentially increasing number of scientific publications and the "*publish-or-perish*" imperative may discourage new scientific researchers from exploring seemingly esoteric ancient bibliographies. The pres-

ent work reinforces the idea that the research of Lacaze-Duthiers was not only remarkable in its time and is being validated today but also can remain a source of inspiration for studies on the red coral, an organism of which Lacaze-Duthiers said that *"nothing is as pretty and delicate as these little beings…"* (HLD, p. 176) in speaking of newly-settled coral recruits.

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Mrs J Carpine-Lancre, historian of oceanography dedicated her professional life to the study of the work of Prince Albert I of Monaco. She helped one of us (D A) in the preparation of the conference dedicated to Henri de Lacaze-Duthiers that was held at Banyuls-sur-Mer in July 2021. She expressed her interest in the resulting paper. Unfortunately, she never got to read it as she died February 21st, 2022. This article is dedicated to her memory.

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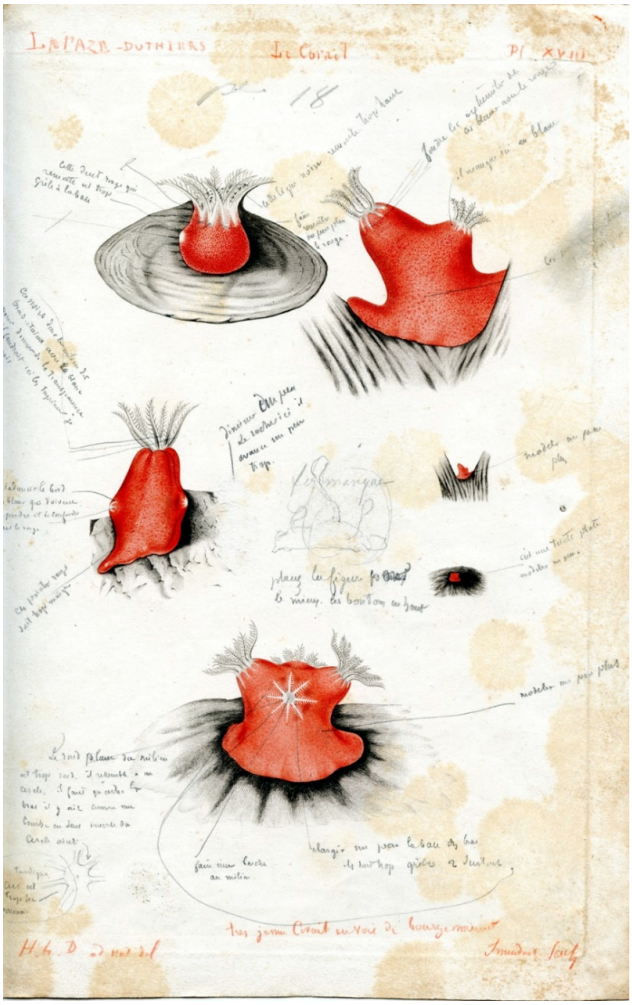
Supplementary materials

HENRI DE LACAZE-DUTHIERS' CORAL PLATES

The text of Lacaze-Duthiers' monograph is illustrated by twenty colored plates assembled at the end of the book. All plates mention the name of the publisher (Librairie J.B. Baillière et Fils. Paris) and the printer (Imp. A. Salmon, 15 Rue Vieille Estrapade, Paris), and are signed in the lower left corner with an H.L.D. ad nat. del. (H. Lacaze-Duthiers, drawn after nature) and at the bottom right of an Annedouche sculp. (Annedouche Joseph Alfred – 1833-1922, engraver). The original watercolors would thus be by Lacaze-Duthiers and the engraving work for the printing would have been done by J.A. Annedouche. In order to put more emphasis on HLD's drawings, the above mentioned signatures in the upper and lower parts of the plates have not been included in the digitizations, except in Plate XV.

The digitizations of the plates of the work of Henri Lacaze-Duthiers were made in part by SCD Aix-Marseille University - Health Department. Library of Medicine-Odontology. La Timone (Marseille, France), in part at Arago laboratory of Banyuls-sur-Mer. We thank Sophie Astier from Marseille for her precious help. We thank the Library of the Arago laboratory of Banyuls-sur-Mer (Sorbonne University) to have granted us a right of reproduction of an original plate of Professor Henri Lacaze-Duthiers, preserved in its patrimonial fund.

The legends of the plates are those of Lacaze-Duthiers translated in English by us. For clarity, some old terms used by Lacaze-Duthiers have been replaced by their modern equivalent.



Reproduction of a version of plate XVIII in preparation, with handwritten annotations by Lacaze-Duthiers. Compare with the final plate XVIII presented below. Collection of the library of the Oceanological Observatory of Banyuls-sur-Mer.

PLATE I. CORAL EXPANDED, OF NATURAL SIZE AND ENLARGED.

Fig. 1. Puntarella or tip of a zoanthodeme of natural size, contracted, having lived two and a half months in the aquariums.

Fig. 2. The same swollen a few moments before the blooming; the polyps appear as small white dots. This must be the state that earlier authors meant, when they said that the stems were covered with small droplets of milk.

Fig. 3. Other end of a zoanthodeme of natural size, with the polyps expanded to show the relative size of the animals.

Fig. 4. Portion of the same one, enlarged, intended to show the shape of the bulges of the coenenchyme[1] which follow the retraction of the polyps.

Fig. 5. This figure represents in all its expansion the puntarella, fig. 1 and fig. 2, very enlarged and during its blooming. If one compares it to figure 3, one can notice that the body of the polyps is much less elongated and that the 'stars' seem to come directly out of the coenenchyme. This is one of the many differences that one will notice very quickly when observing the living coral.

[1] Lacaze-Duthiers uses the term 'sarcosome' instead of coenenchyme.

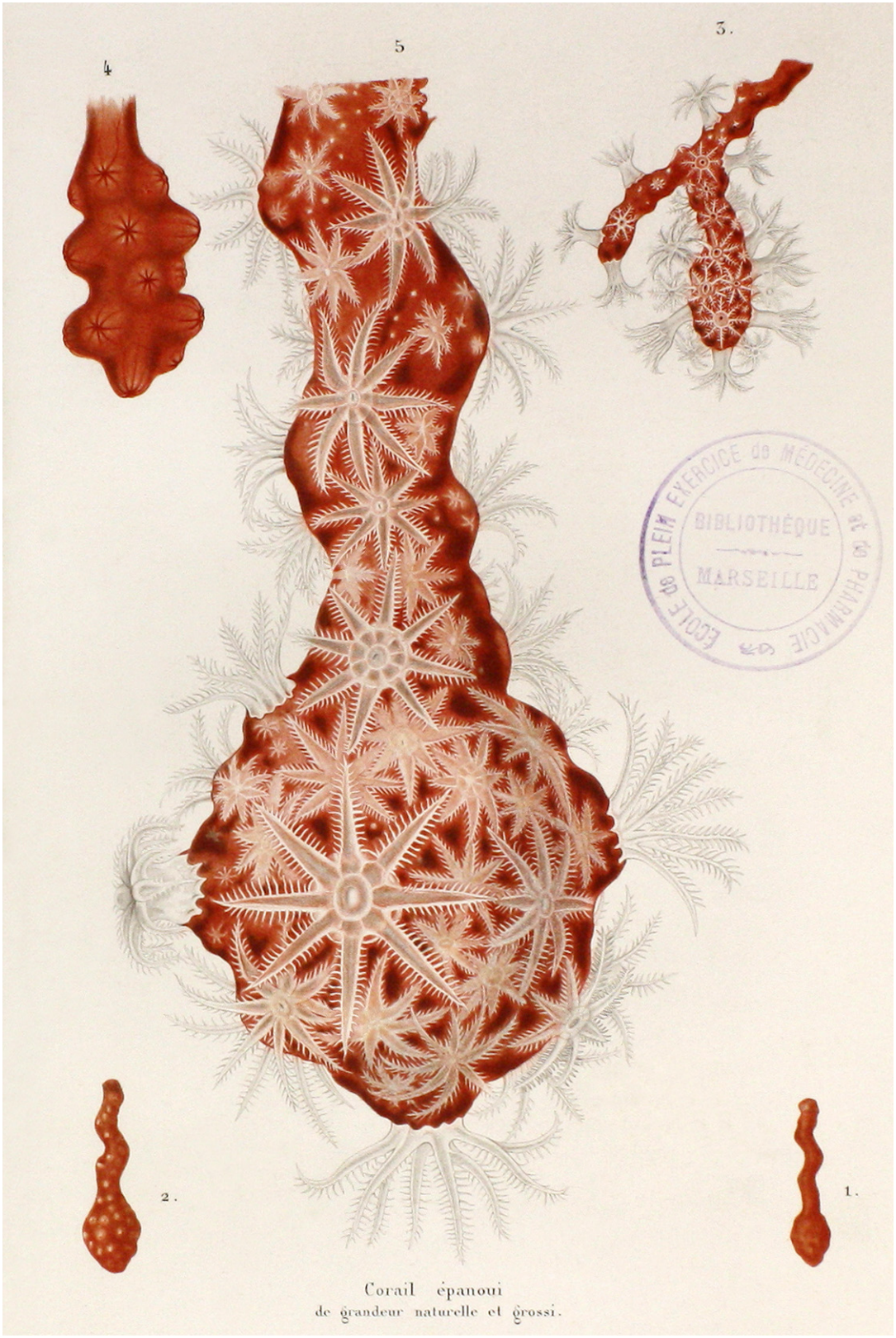

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Plate I

PLATE II. SHAPE OF THE POLYPS AND THEIR TENTACLES.

Fig. 6. Three polyps extended and expanded to different degrees. A, polyp coming out of the calyx [the reinforced rim of the anthostele] of the coenenchyme *(a)*; B, animal less extended than the one in C, it shows on its body, below each tentacle, a small bulge *(b)*, corresponding to the tooth of the calyx of the coenenchyme. In the individual C one sees a streak *(i)*, it is the esophagus [siphonoglyph]; the mouth appears in *(k)*.

Fig. 7. An isolated polyp showing one of the most common appearances. Beneath the tentacles [HLD often uses the term 'arm'] is a constriction *(c)*, then a ventral portion *(d)*. On the white body, there are a few red spicules *(e)*. This fact is quite rare. One can notice in this same figure how clearly the separation of the coenenchyme and the body of the polyp is marked.

Fig. 8. Polyp offering a shape quite different from that seen in the preceding figure; the coenenchyme does not rise in a tube, the body is cylindrical, the tentacles are spread out in a wheel and the pinnules [pinnae] of the tentacles are folded back below: *(k)* mouth; *(c)* circular wrinkle.

Fig. 9. A tentacle magnified to show *(f)* the smallest pinnules [HLD uses the term 'barbule'], located on the upper surface, on the side of the mouth: *(g)* the larger ones in the middle; *(h)* those at the end.

Fig. 10. The same more strongly magnified and seen in profile. It can be seen very well in this position that the pinnules are obliquely directed from top to bottom and from inside to outside that the first *(f)* are the smallest and look like tubercles. NOTA: To appreciate the description in the text [HLD's book], it is useful to turn the plate so as to place this tentacle horizontally.

Fig. 11. Enlarged pinnule, showing its internal cavity occupied by a brownish material.

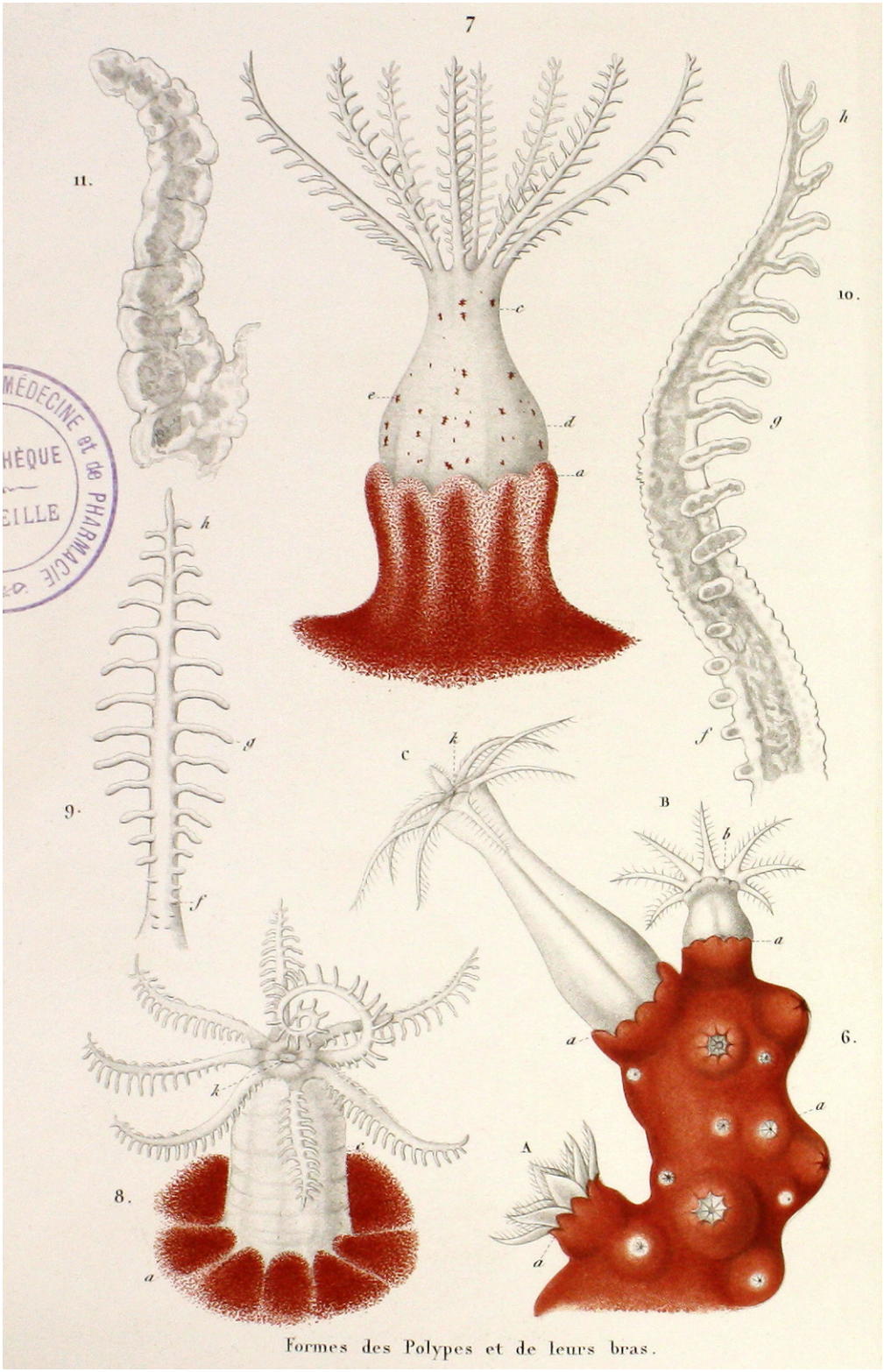


Plate II

PLATE III. INTERIOR OF THE POLYPS. – HISTOLOGY OF THE TENTACLES.

Fig. 12. End of a pinnule magnified 500 times: *(i)* outer layer of cells; *(h)* large cells forming the inner network and bearing the vibratory [ciliated] epithelium.

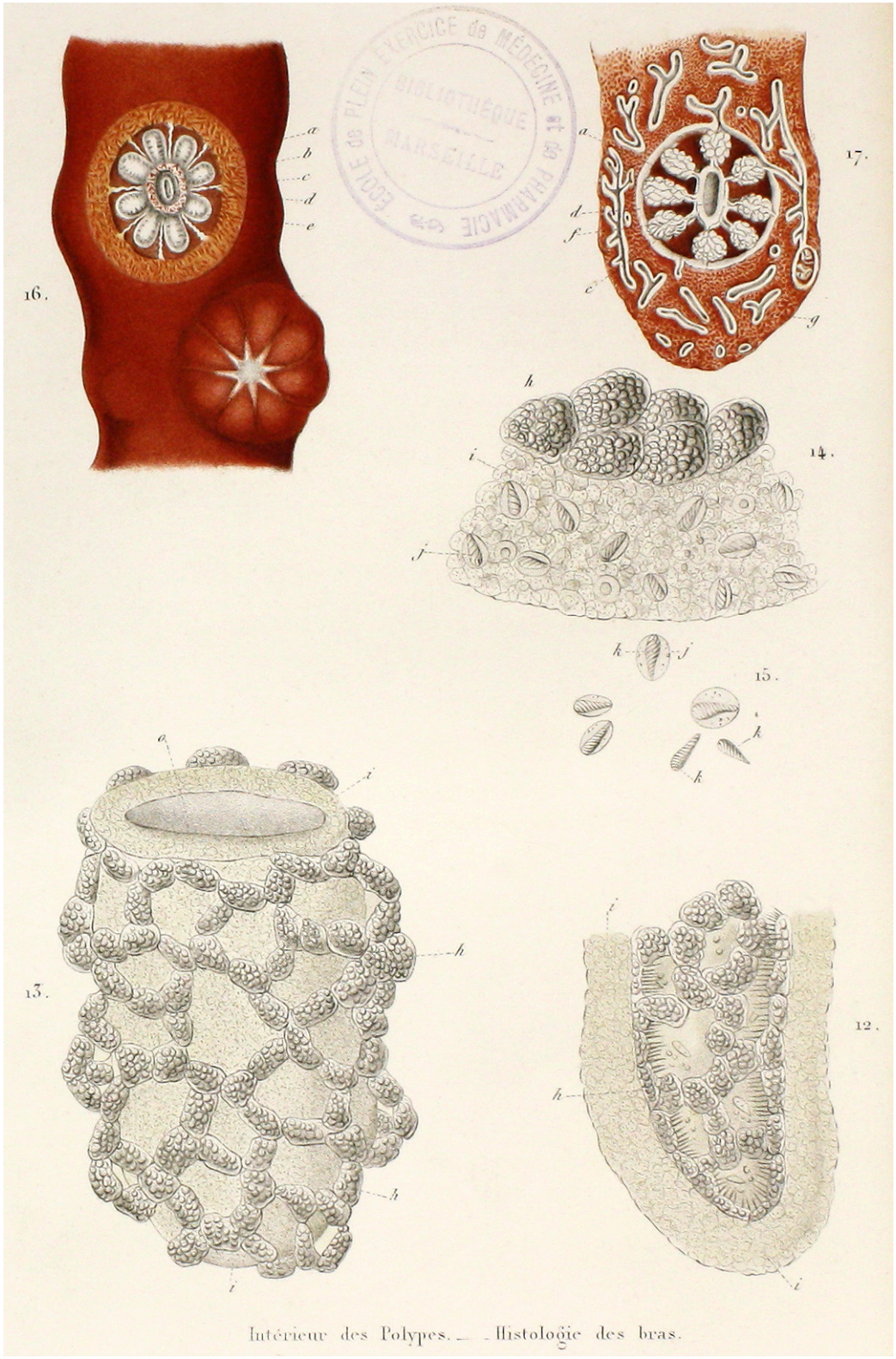
Fig. 13. Pinnule turned upside down by the contractions referred to in the text: *(i)* outer layer of cells now inward; *(h)* cells with large granulations and vibratory cilia, forming the inner layer and enveloping the pinnule with a veritable meshwork.

Fig. 14. Portions of the wall of a pinnule magnified 700 times: *(i)* elementary cells of the outer layer; *(j)* nematocyst.

Fig. 15. Isolated, highly enlarged nematocysts: *(k)* inner capsule with spiral thread; *(j)* mother cells surrounding the nematocyst.

Fig. 16. Coral stem on which a horizontal section shows: *(a)* the periesophageal lodges; *(b)* the upside-down tentacles occupying the periesophageal cavity; *(c)* the partitions [mesenteries] dividing the gastrovascular cavity; *(d)* the mouth; *(e)* remnant of the calyx of the coenenchyme.

Fig. 17. Section similar to the previous one, but made deeper: *(a)* body wall; *(c)* septum [mesentery]; *(f)* intestinal folds [mesenteric filaments?]; *(d)* mouth; *(g)* vascular canals of the coenenchyme.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Intérieur des Polypes. — Histologie des bras.

Plate III

PLATE IV. EPIDERMIS. – COENENCHYME. – AXIS.

Fig. 18. Portion of a stem with the bark [coenenchyme] split along the length and partly removed.
– B, B', B", polyps opened and seen in different positions.
– B, Polyp with tentacles expanded: *(k)* mouth, one lip preserved; *(m)* esophagus [pharynx]; *(i)* lower esophageal bulge or sphincter; *(j)* radial or mesenteroid folds [mesenteric filaments].
– B', polyp with retracted tentacles that appear in *(d)* periesophageal lodges: *(e)* circular space around mouth and pharynx; *(c)* orifice corresponding to inverted tentacles; *(b)* part of body forming the protruding tube [anthocodia] when expanded; *(a)* festoons of calyx.
– B", polyp cut deeply and showing the eight radiating septa [mesenteries] or folds, free toward the middle of the cavity.
– A, A, coenenchyme with its canals in irregular arrays *(h)*; or in longitudinal tube arrays *(f)*.
– P, Axis: *(g)* its grooves along which the longitudinal gastrodermal canals run *(f)*.

Fig. 19. Portion of epidermis detached from surface without appreciable structure, and released sclerites *(j)*, cells *(k, i)*.

Fig. 20. Adult zoanthodeme that no longer appears to increase in length and whose blastozoites [blastozooids] are large and widely spaced especially toward the base.
– E, portion of epidermis detached from coenenchyme. It is this portion that is seen magnified in figure 19.
– A, bark [coenenchyme] separated from the axis and the polyps, to show the latter still attached to the axis.

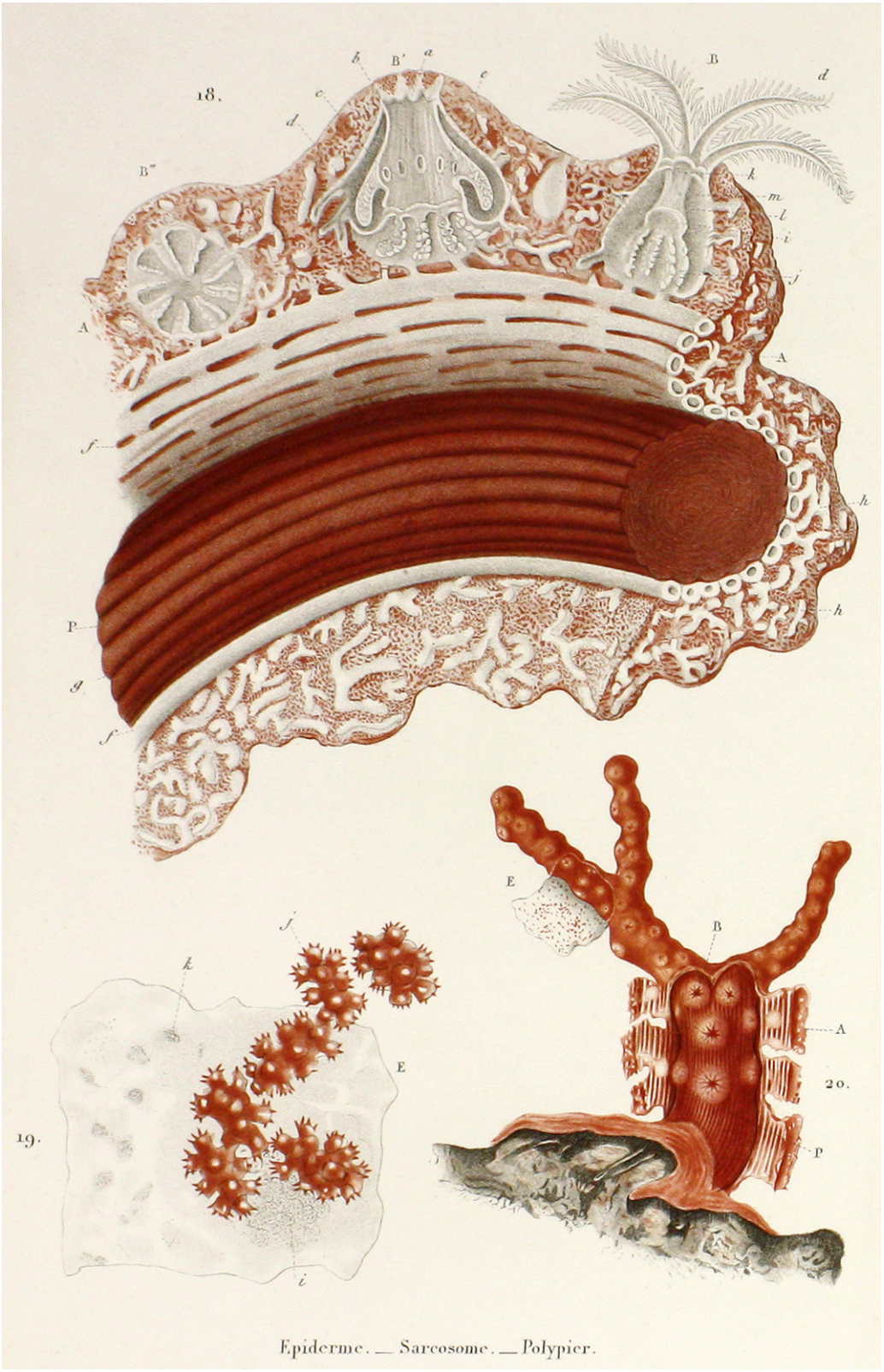

Plate IV

PLATE V. APPARATUS OF THE CIRCULATION.

Fig. 21. Coral prepared by means of putrefaction. Two orders of canals are distinctly seen exposed by means of a stream of water which has carried away the tissue and spicules of the coenenchyme.
P, axis: *(a)* longitudinal canals; *(b)* irregular networks; A, intact coenenchyme; B, polyp contracted at the top of the figure. This drawing gives a very exact idea of the relations of the parts which compose a zoanthodeme [branch].

Fig. 22. Portion of coenenchyme detached from the axis and seen by its inner face: *(a)* longitudinal canals; *(d)* transverse anastomotic vessels establishing communication between two parallel canals; *(b, e)* irregular networks more or less superficial and deep; *(c)* orifice for communication of the two orders of canals. B, place occupied by a polyp; A, thickness of the coenenchyme; *(x)* small white corpuscles often found around animals and whose nature has not been determined.


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Plate V

PLATE VI. TISSUE AND SCLERITES.

Fig. 23. Thin section of coenenchyme tissue, seen at 500x magnification.
B, inner wall of the body of an adult polyp, it is loaded with vibratory cilia and formed of granular cells: *(b, b)* canals cut perpendicular to their direction; *(e)* canals leading from the cavity of a B polyp into the irregular meshwork. In the tissue of the coenenchyme are fairly regularly spaced spicules placed at different depths, they are embedded in a partly cellular and partly transparent tissue without a clear structure.

Fig. 24. Sclerites drawn at 500x magnification: *(b)* position that the spicules must be given to be able to follow the description in the text; *(a)* the same as in *(b)* seen a little sideways, to show how much the appearance changes by a slight displacement.

Fig. 25. Terminal spinule nodes of the most regular spicules that can be encountered, and showing the eight rows of spines[2] that cover them; in *(a)* they are seen from the front, by their extremity, and in *(b)* in profile.

Fig. 26. (a, b, c) three sclerites seen at the same magnification as those of figure 24 and in the process of development, each of which represents very exactly two isosceles triangles superimposed.

[2] Probably an erroneous observation.

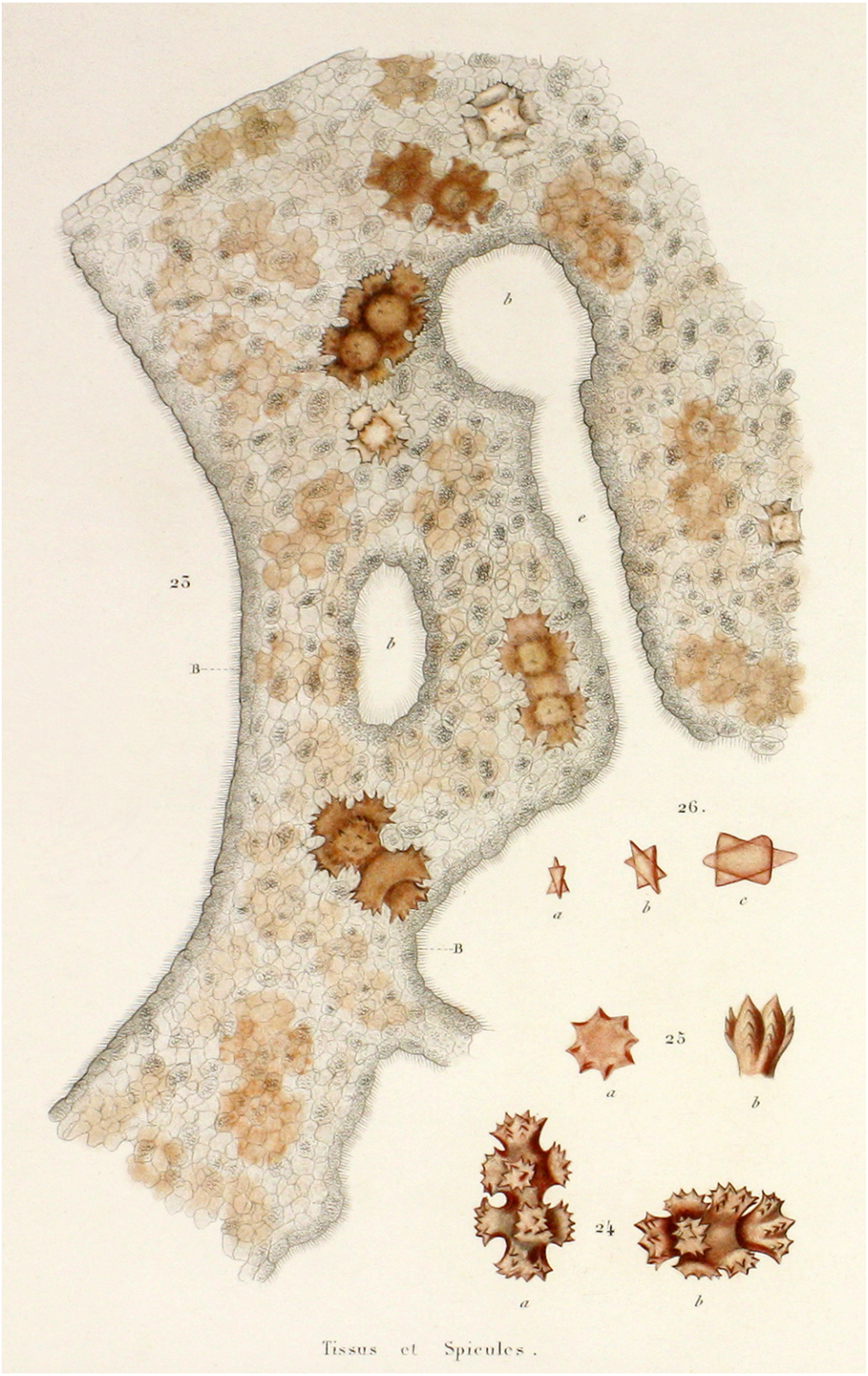

Plate VI

PLATE VII. BUDDING AND BLASTOGENESIS.

Fig. 27. Zoanthodeme whose animals had been killed by the development of a Bryozoan T, but which recovers and begins to cover it with a layer of coenenchyme S. In P the axis of the primitive formation is seen.

Fig. 28. Portion of the coenenchyme layer, covering the Bryozoan in the previous figure and inverted to show the superficial vascular network *(a)*, whose vessels are much larger than those seen below *(b)*.

Fig. 29. Basilar portion of a broken zoanthodeme, the ends of which are covered by newly formed coenenchyme, and in the middle of which rises a young tigella [new branch]. If one compares figure 10 of Plate IV with the drawing of this colony of Coral, one sees that the polyps offer the same size: but in one case they present between them numerous small white points, while in the other they do not offer any. This is because, in the latter example, the blastogenetic force has been awakened by the accident that happened to the zoanthodeme, and the repair is in progress. A broken axis can thus continue, not only to live, but also to expand.

Fig. 30. Portion of a stem with very large blastozooids D, surrounded by young polyps forming as many white spots B'. It is these dots that look like pores.

Fig. 31. Two white points B' of the preceding figure seen at a higher magnification. It can be seen very clearly, by thus increasing the magnifying powers, that each of these pores presents the eight characteristic rays of the calyx of the coenenchyme. They cannot therefore be considered as particular orifices; they correspond to the mouths of young blastozooids.

Fig. 32. Portion: of the coenenchyme showing, around a polyp, six young blastozooids from B' to B".

Fig. 33. Blastozooid B" of the preceding figure seen at a fairly high magnification and showing the part *(b)* or white tissue which develops to form the polyp.

Fig. 34. A more advanced blastozooid, the red tissue *(a)* begins to break away and leave the central part (b) exposed.

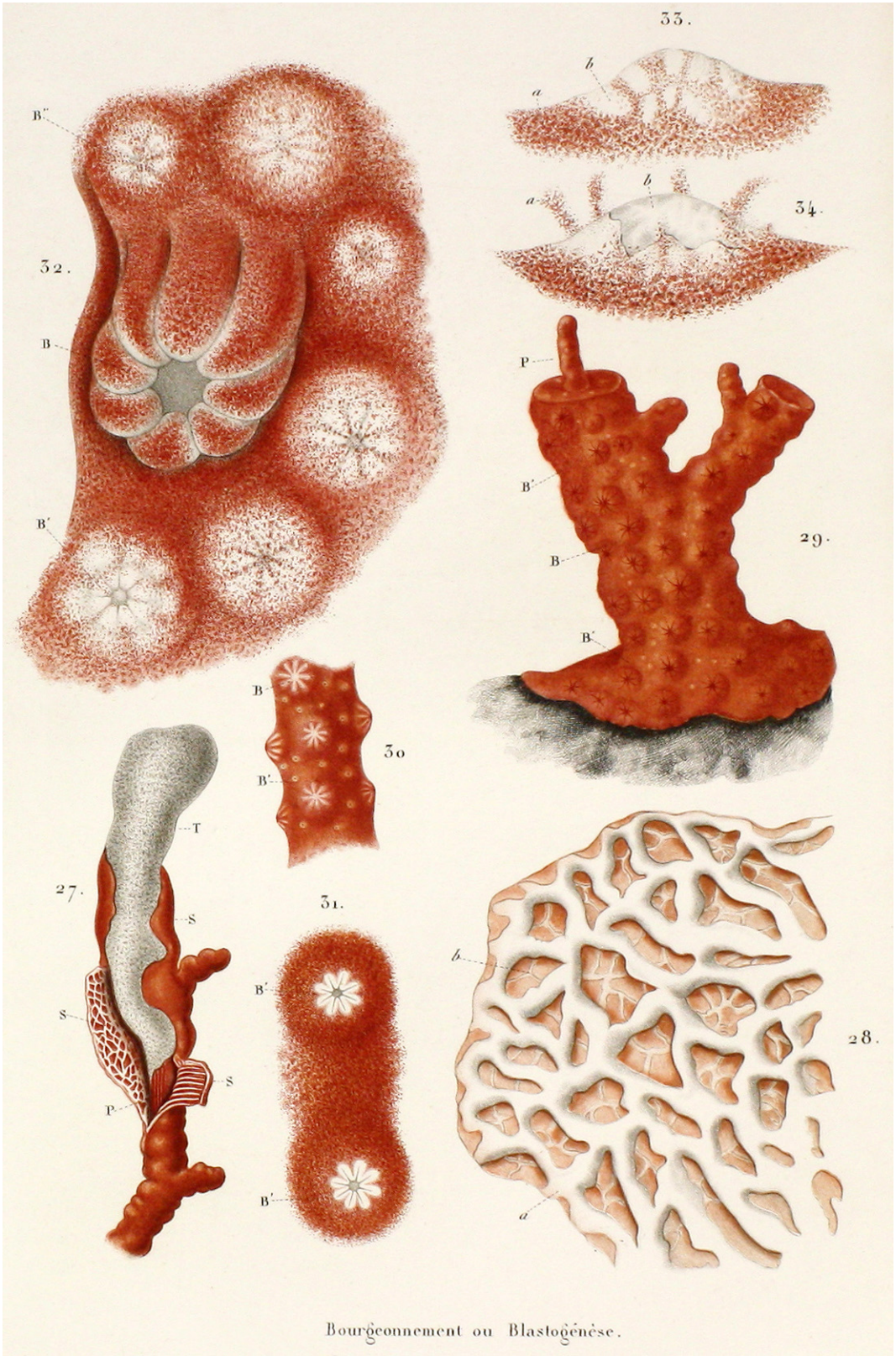
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Plate VII

PLATE VIII. STRUCTURE OF THE AXIS.

Fig. 35. End of a stem from which a portion of the coenenchyme has been removed, in order to show the position of the axis (P), still in the form of irregular, interrupted, and separated blades, in the midst of the soft tissues and polyps (B).

Fig. 36. Axis in the process of formation, as found in the interior of a branch tip. It is lamellar and pierced with holes resulting from the welding of the bundles or agglomeration of sclerites, which are forming in the surrounding tissues; *(f)* bundles of isolated calcareous corpuscles not yet welded to the lamella; the holes or free spaces *(e)* are the consequence of the welding and joining of the sclerite aggregates*(f)*.

Fig. 37. Thin section of a skeleton cut perpendicular to the axis and showing: *(i)* more colored and contoured ribbons, leaving a space between these two lamellae occupied by a grayish material *(j)*. This ribbon represents the first shape that the axis had in the end of the branches, as, for example, in figure 35.

Around this central and irregular part, the calcareous matter was deposited so as to make the axis perfectly cylindrical; it presents rays alternately redder and less colored. These last ones offer fine blackish striations *(h)*, which correspond exactly to the bottom of the grooves that one sees on the surface of the branches. The more colored bands *(g)* correspond to the top of the ridges that separate the grooves.

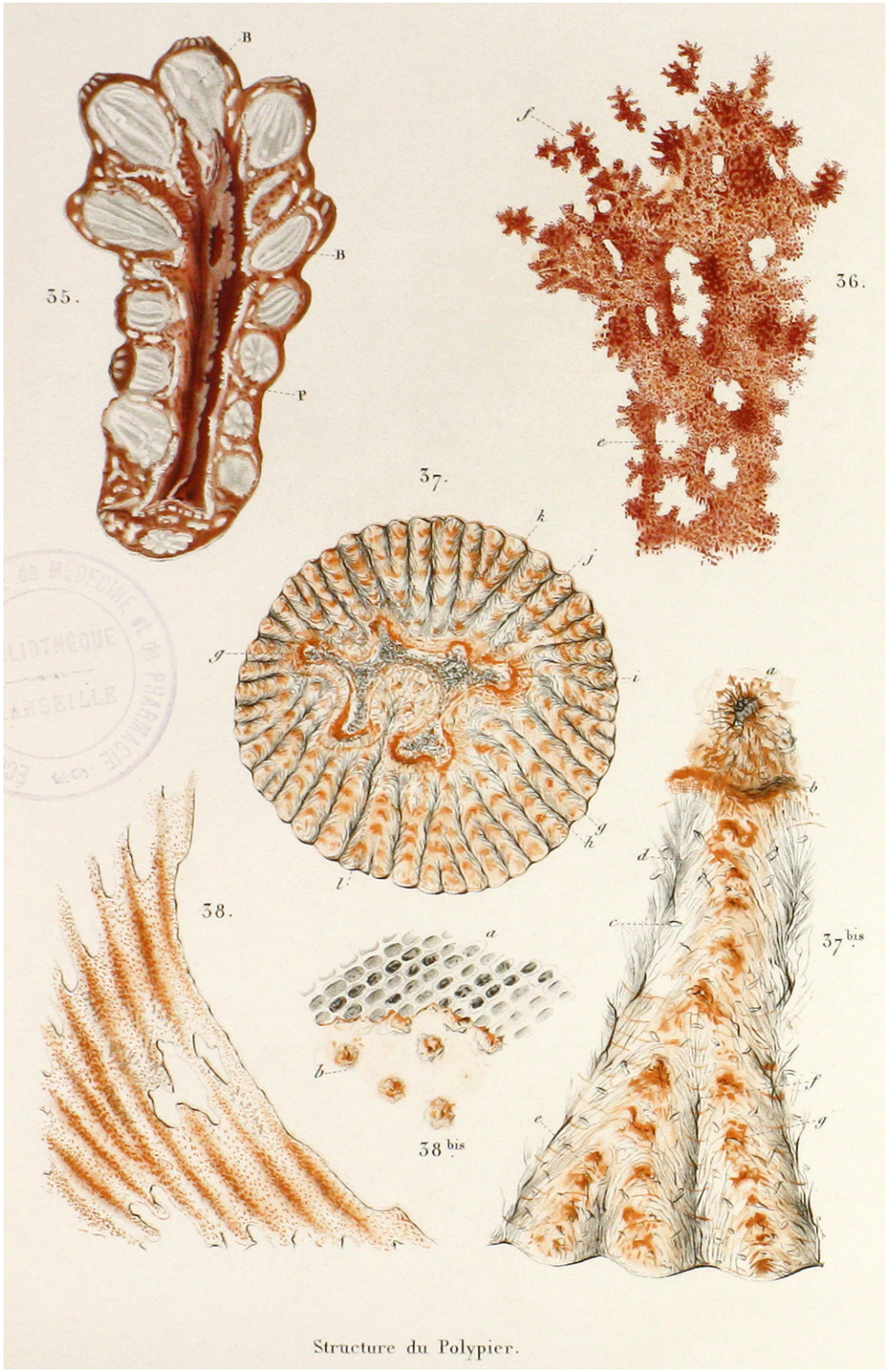
From far away, one can notice that these radiating bands bifurcate at different heights.

Fig. 37 bis. One of the rays in the previous figure seen at 200x magnification: *(a, b)* central ribbon; *(g)* spots of brighter colors; *(d)* lighter space covered with small black streaks; *(e, f)* two bifurcations of the ray; (c) peculiar corpuscles which appear to be the cores corresponding to the spicules encompassed by the cement which formed the stem.

Fig. 38. Portion of axis cut parallel to the surface and showing the inequality of coloration corresponding to the top of the ridges *(d)* that separate the furrows *(c)*. In this figure, one clearly distinguishes a dotted surface with very small red spots, each corresponding to a sclerite[3].

Fig. 38 bis. Blades of melobesia *(a)* thinned to uncover a layer of coral that covered it and in which one sees the origin of the sclerites *(b)*.

[3] It seems likely that Lacaze-Duthiers confuses sclerites with microprotuberances.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Structure du Polypier.

Plate VIII

PLATE IX. MALES AND FEMALES. - SPERMATOZOA.

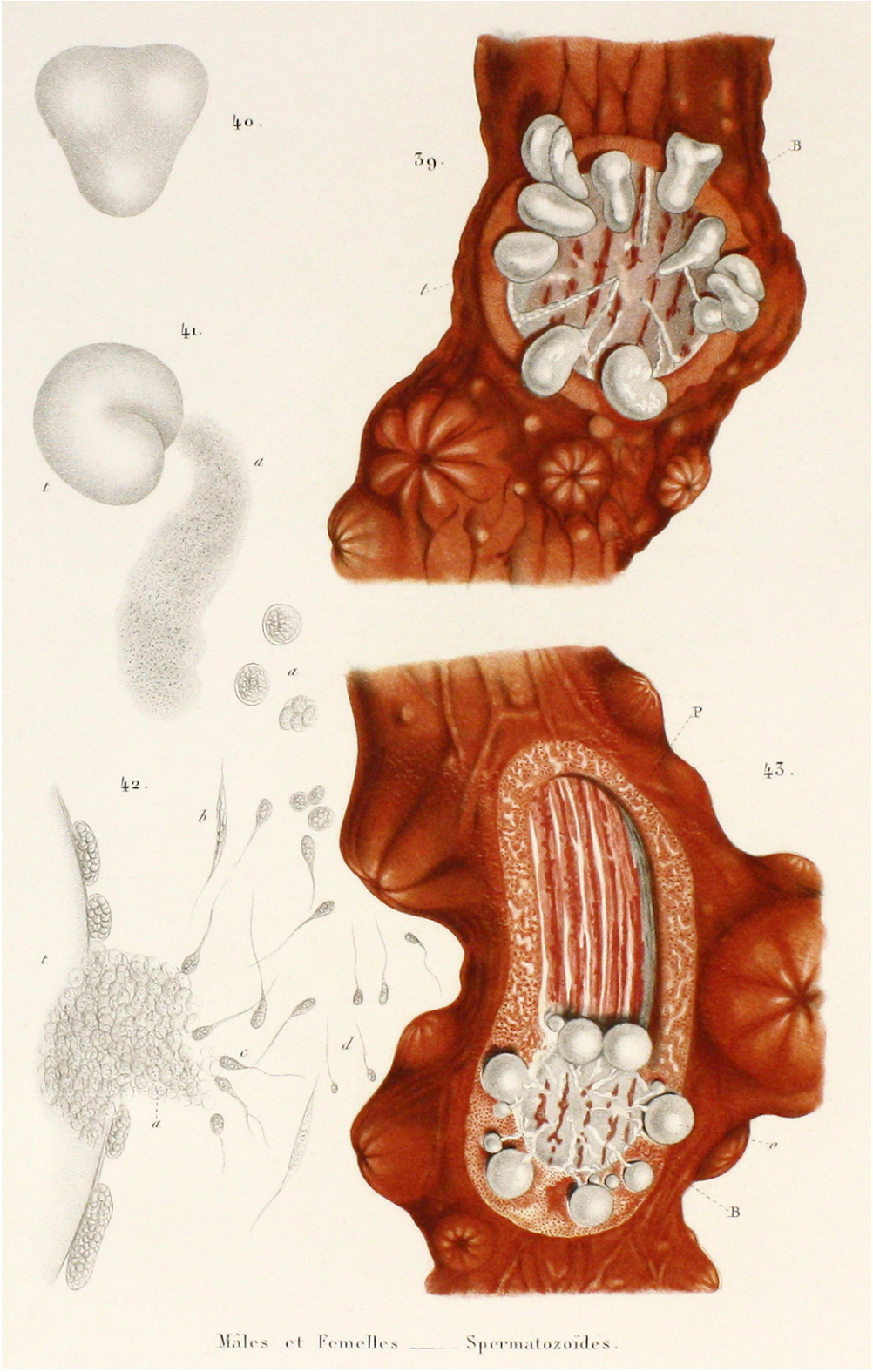
Fig. 39. An open polyp B to show the shape and arrangement of the male glandular capsules attached to the radiated folds mesenteries of the central cavity.

Fig. 40. An isolated, turgid male capsule.

Fig. 41. Male capsule in mature state and ruptured by endosmosis, *(a)* cloud of seminal material escaping from it.

Fig. 42. The same, seen at 500 times magnification: *(a)* characteristic, sperm-producing cells that are more or less free and clear of the capsule from *(b)* to *(c)* and *(d)*.

Fig. 43. Female polyp open and showing perfectly spherical eggs in various stages of maturation.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Mâles et Femelles ____ Spermatozoïdes.

Plate IX

PLATE X. FORMATION OF THE EGGS.

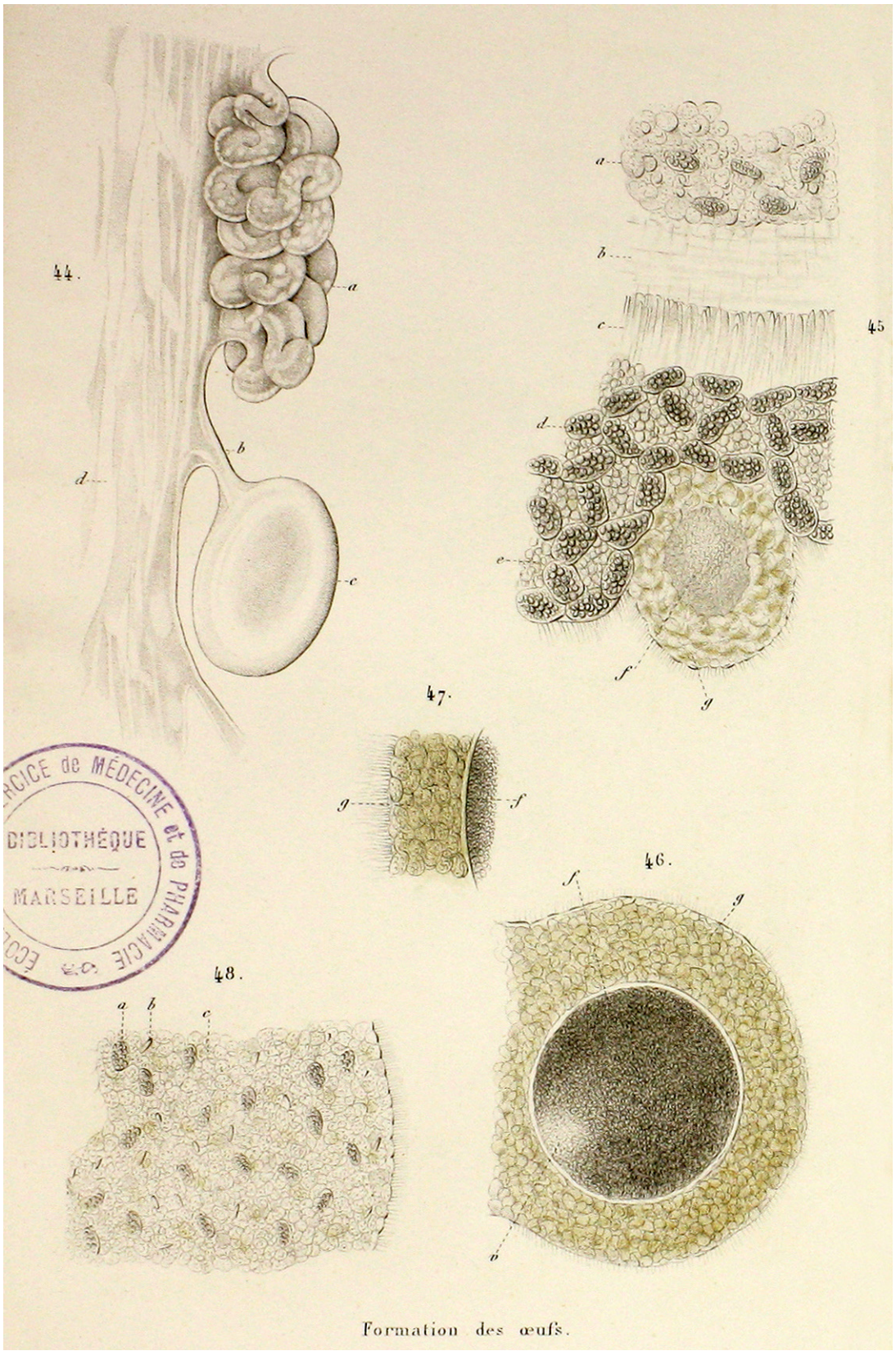
Fig. 44. A radiating or fold mesentery seen in profile, to show the position of the egg *(c),* suspended from the blade [mesentery] *(d),* by a pedicle *(b)*, below a twisted bulge *(a)* reminiscent of the convolutions of an intestine.

Fig. 45. Portions of the radiate fold mesentery, seen at 500 times magnification, showing a fibrous central part *(b, c)*, an outer layer *(a)* and *(e)*, on which is a network *(d)* of cells with large granulations similar to those seen in the inner arms [tentacles]; *(f)* is a forming egg surrounded by a cell capsule *(g)*.

Fig. 46. A more developed egg: *(g)* cell capsule; *(f)* yolk; *(v)* clear space corresponding to the germinal vesicle.

Fig. 47. Part of a larger egg than the previous one: *(f)* yolk; *(g)* cell capsule covered with vibratory cilia.

Fig. 48. Portion of the twisted bulge, seen at high magnification: *(a)* granular cells; *(b)* nematocysts; *(c)* slightly yellowish cells mixed with the small and delicate cells that form the rest of the bulge.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ÉCOLE SUPÉRIEURE de MÉDECINE et de PHARMACIE
BIBLIOTHÈQUE
MARSEILLE
Formation des œufs.

Plate X

PLATE XI. ELEMENTS OF THE EGG. - HERMAPHRODITISM.

Fig. 49. Portion of a radiated [mesentery] fold *(r)*, bearing: (1) in *(o)* an egg, the capsule *(a)* of which has partly fallen off, the yolk *(b)* of which shows a very marked clearing *(d)*, corresponding to the transparent vesicle, and in the middle of which are the germinal spots *(c)*; (2) in *(e)* a developing capsule, remarkable for a space which seems empty *(g)* surrounded by a cellular band *(f)* which a capsule *(e)* imitates; this is a testis.

Fig. 50. Elements of the yolk *(a)* striated part, formed by the folding of the yolk capsule; *(b)* fatty granulations forming the yolk.

Fig. 51. Portion of an egg that has died and turned yellow, its yolk exuded in the form of large oily droplets *(i)*.

Fig. 52. Two opened polyps belonging to the same coral stem; one of them (B) is female and contains only eggs *(o)*, the other B' presents its radiated folds mesenteries *(r)*, compressed by an egg *(o)* and a male capsule *(e)*. It is thus hermaphrodite.

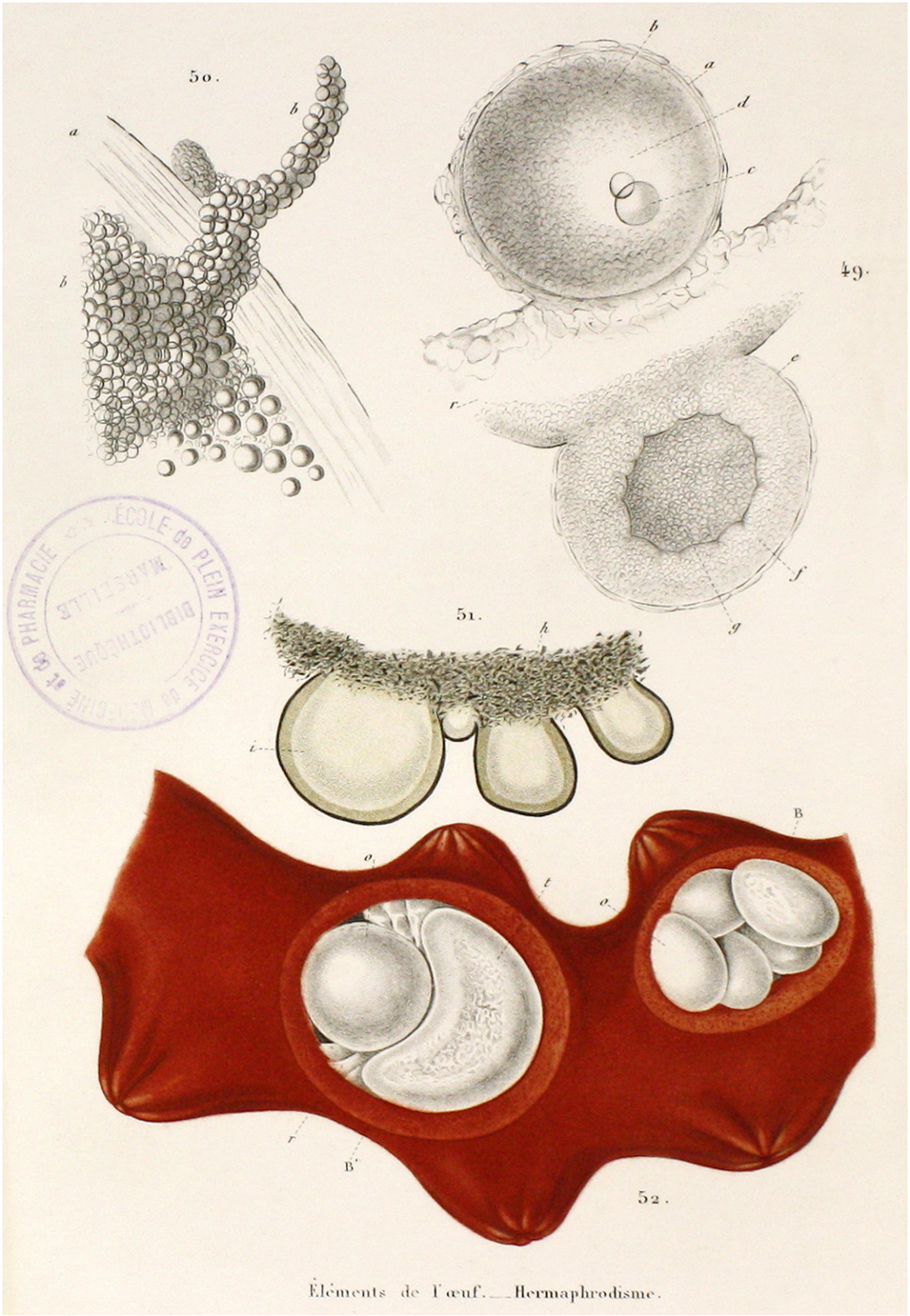

Plate XI

PLATE XII. CORAL THROWING ITS SEED. - MILK. - CAPSULE OF THE EGG.

Fig. 53. Mature egg: *(d)* pedicel; *(e)* capsule torn open and showing egg *(f)*.

Fig. 54[4]. Portion of the egg capsule to show its structure: *(h)* cells forming it covered with vibratory cilia *(g)*; yolk *(i)*. Magnification, 500 diameters.

Fig. 55. Portion of a milk droplet from Coral where all the elements are found together: *(m, e)* granular cells; *(n)* sclerite; *(o)* indeterminate rods; *(p)* very-small granulations.

Figs 56, 57, 58, 59, 60. Elements found in the milk of Coral, more or less united; fig. 56, egg not very developed, exceptionally offering a pink tinge.

Fig. 57. *(q)* Cells lining the vessels; *(r)* nematocyst.

Fig. 58. *(j)* Indeterminate rods; *(k)* poorly developed spicules.

Fig. 59. Cells lining the inner surface of the arms.

Fig. 60. Miscellaneous cells and granulations.

Fig. 61. Male colony of natural size; one sees below him the white clouds that form the seed thrown by some polyps.

[4] Erroneously numbered 51 in HLD's plate XII..


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Mâles lançant la semence.
Lait. — Capsule de l'œuf.

Plate XII

PLATE XIII. BIRTH OF THE LARVAE OR EMBRYOS.

Fig. 62. Exit of the larvae, in the form of planulae, during the contraction of the polyps.

Fig. 63. Portion of a Coral branch showing in B a larva escaping backwards through the mouth of its mother; C, a contracted polyp in which embryos are seen by transparency; in D, the larvae become free, the polyp has been opened.

NOTE. – We have seen in figure 7, plate II, some sclerites sown here and there, in the thickness of the wall of the body of the animals above the limit of the coenenchyme; here the fact is much more striking, it recalls what is so marked in many other Alcyonaria.

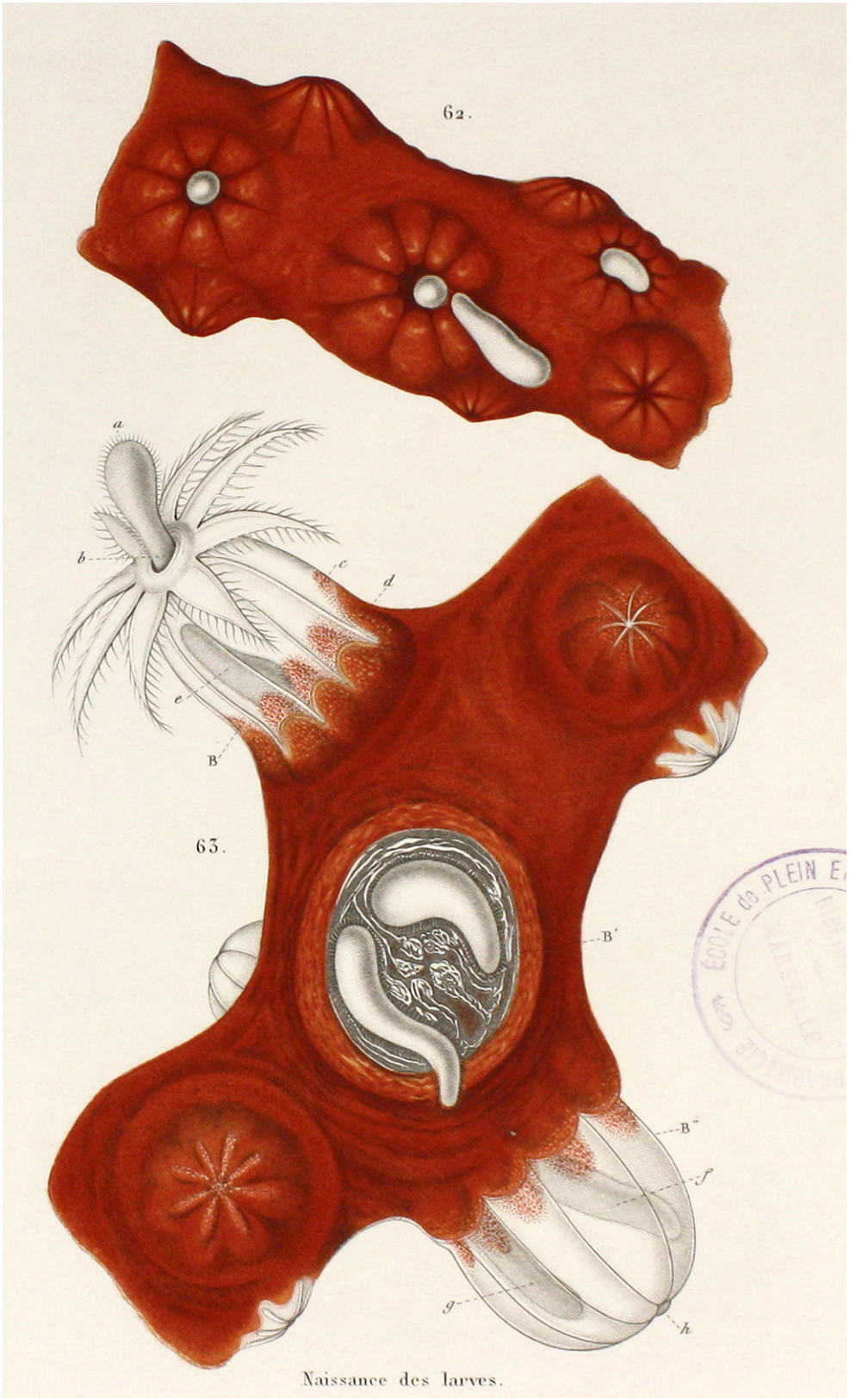
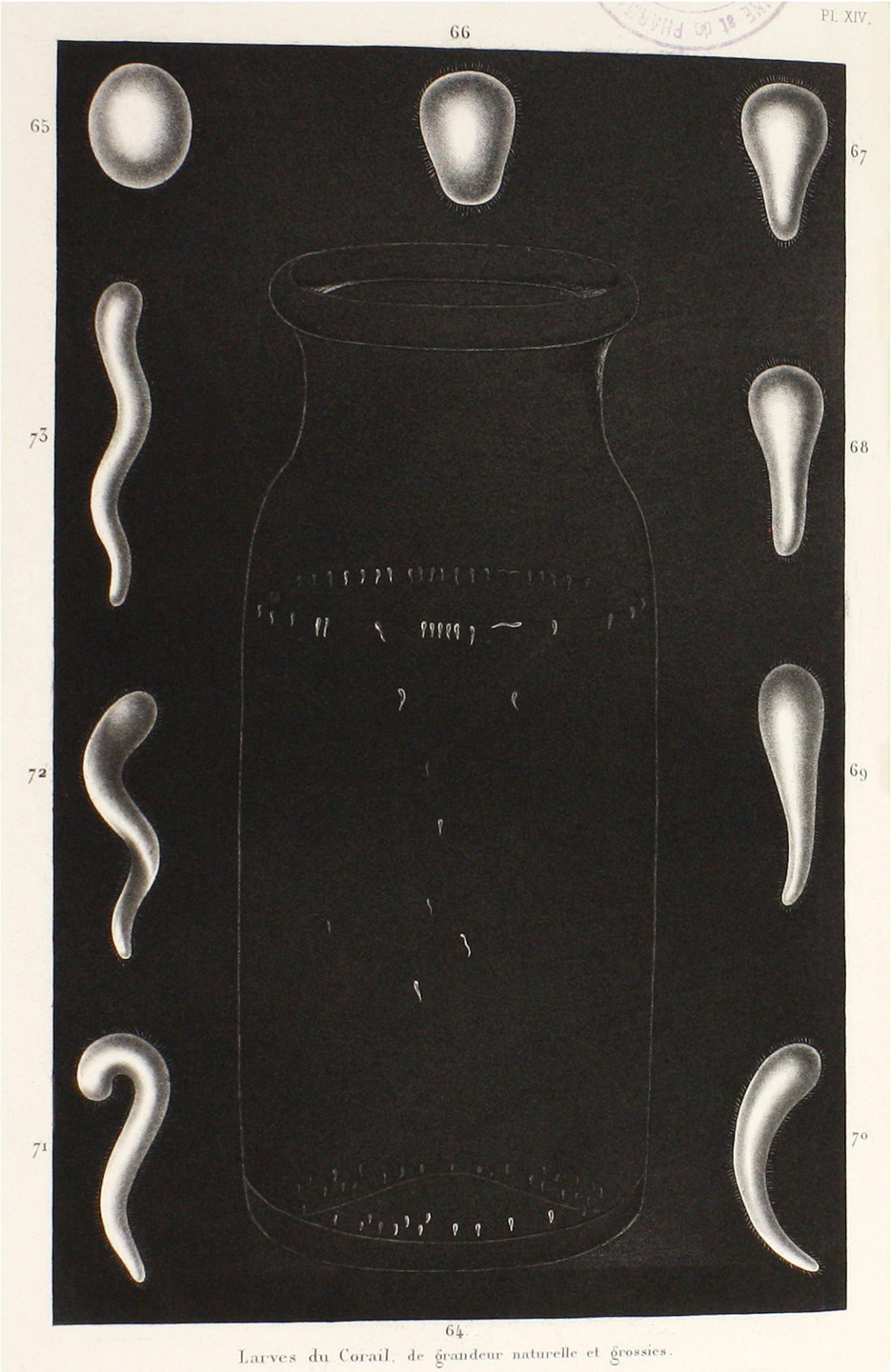


Plate XIII

PLATE XIV. LARVAE OF THE CORAL OF NATURAL SIZE AND ENLARGED.

Fig. 64. A jar filled with larvae of natural size. Some rest at the bottom, always maintaining their vertical position. They have their big end at the top; some go up in the liquid by describing turns of spiral, the others, arrived at the surface, remain immobile or, finally, move by directing themselves horizontally.

Figs 65 to 73. All these figures around the jar represent the different magnified forms that the larvae of the preceding figure present, according to whether they are contracted, elongated or more or less developed.


Pl. XIV.
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Larves du Corail, de grandeur naturelle et grossies.

Plate XIV

PLATE XV. METAMORPHOSIS OF THE LARVAE.

Fig. 74. Exceptional form, double monster, having for a single base two oral extremities.

Figs. 75, 76, 77, 78. These figures show the transformations which must be accomplished in the larva so that it passes from the shape of a worm to that of a disc. It is seen that the posterior part *(a)* tends to widen, and that the anterior or oral extremity *(b)* enters, on the contrary, inwards; in this way one arrives at the figures which follow.

Fig 79. Larva completely metamorphosed in a disc and seen in frontal view. In the center one sees a depression at the bottom of which the mouth appears *(b)*.

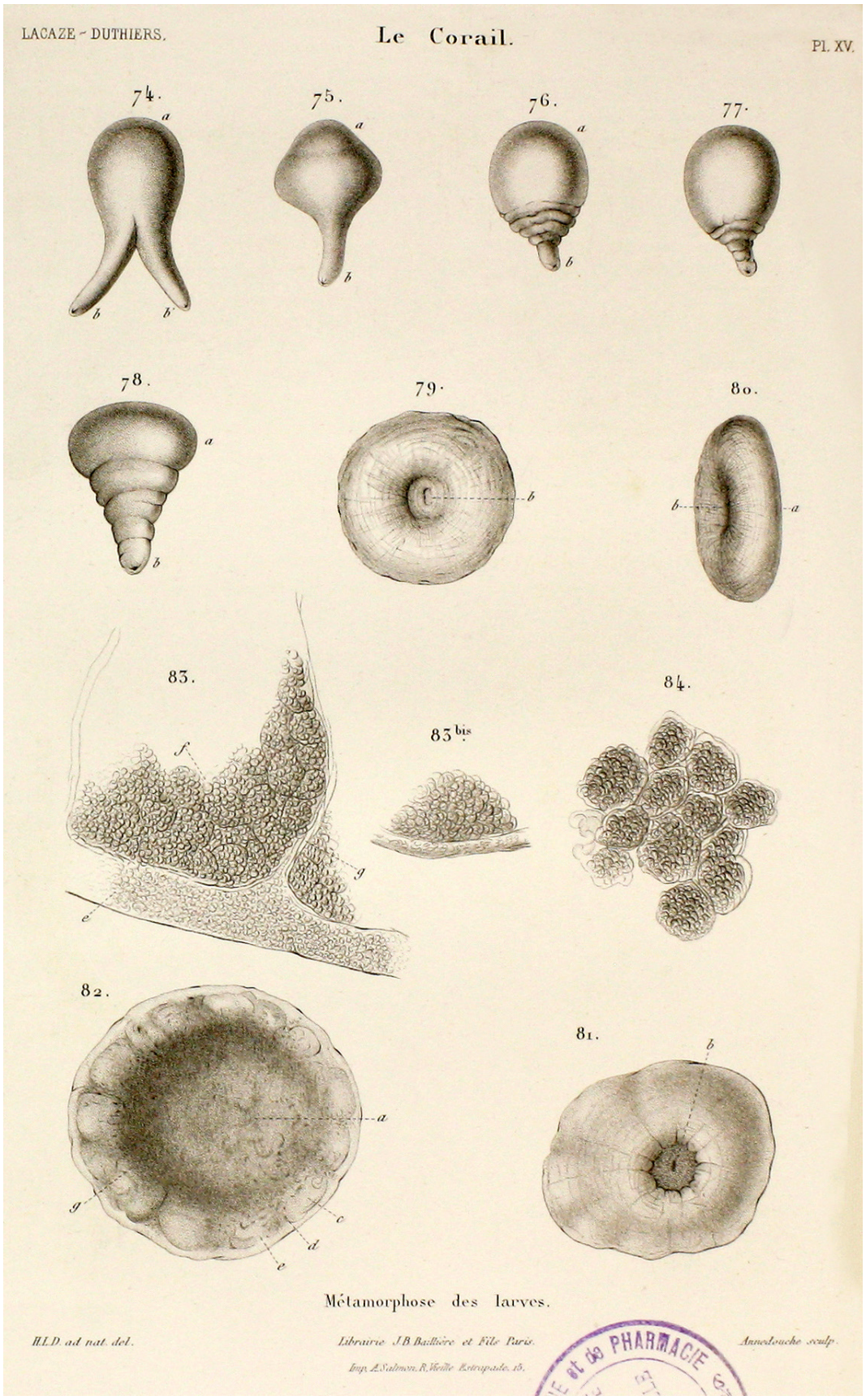
Fig. 80. The same, seen in profile, in order to show the part which corresponds to *(b)* in the preceding figures.

Fig. 81. The same, seen from the front and more developed a few days after its metamorphosis. The central part around the mouth *(b)* is already rising and forming a small bulge; the base is no longer so regularly circular, as it begins to spread over the body which bears it.

Fig. 82. The same, seen from the posterior face *(a)*, as it could be observed by looking with a strong magnifying glass at the wall of the glass vase against which it was fixed. One can already see in its tissue a darker central part *(g)*, lighter parts *(c)* separated by partitions *(d)*.

Fig. 83. Edge of the disc of the previous young oozoid, seen at 300x magnification. The separation of the tissues into two layers can already be seen, one *(f)* formed of very large granular cells, the other composed of smaller cells constituting an external layer *(e)* and extending in the middle of the previous layer by forming a partition.

Fig. 84. Cells *(f)* of the preceding figure, seen at a higher magnification. If we compare them with those of figure 14 *(h)*, plate III, we shall be struck by the similarity which exists between them.


LACAZE - DUTHIERS.
Le Corail.
Pl. XV.
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Métamorphose des larves.
H.L.D. ad nat. del.
Librairie J.B. Baillière et Fils Paris.
Imp. A. Salmon, R. Vieille Estrapade, 15.
Annedouche sculp.

Plate XV

PLATE XVI. HISTOLOGY OF THE LARVAE.

Fig. 85. Larva at the moment of its attachment. A small cloud of viscous matter seems to be deposited towards its extremity *(a)*, which must doubtless serve to facilitate its adherence to solid bodies.

Fig. 86. Oral end of a larva already showing around the mouth *(b)* furrows which correspond to the partitions which are formed in the interior. It should be noted that in the larvae which are represented in figures 69, 70, 71, 72, 73 of Plate XIV, and 74, 75, 76, 77, 78 of Plate XV, by studying them under sufficient magnification, a mouth similar to that just seen here would have been found.

Fig. 87. Portion of a larva analogous to that of figure 85; compressed and torn: *(n)* outer wall; *(o)* appearance of large granular cells; *(p)* appearance of a cell without granulations.

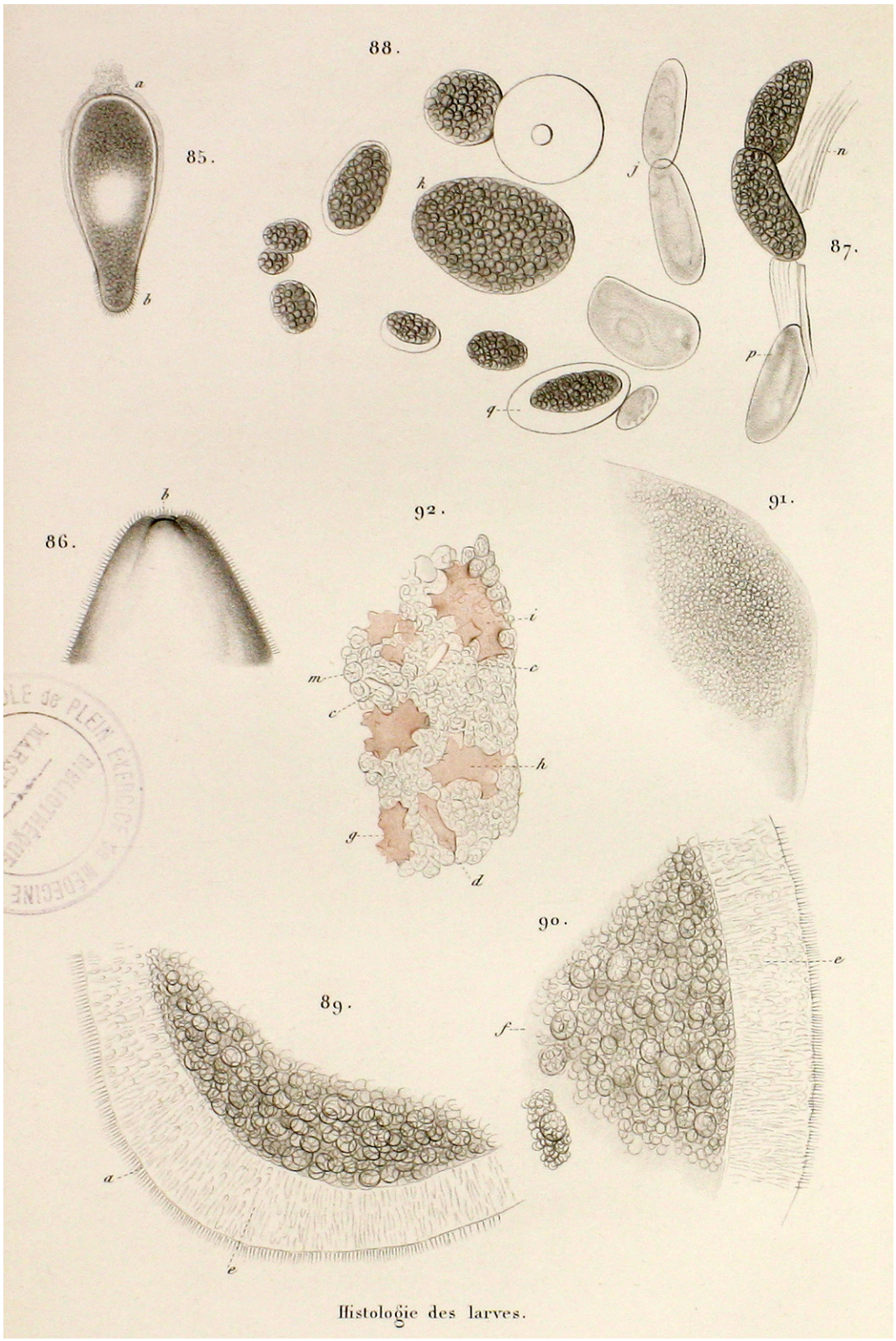
Fig. 88. Corpuscles emerging from a compressed larva. One would think to see sometimes large granular cells *(k)*, sometimes more or less elongated semi-transparent cells *(j)*, sometimes a true germinal vesicle *(l)*, sometimes finally granular cells enclosed in a larger transparent cell *(g)*. All these appearances are due to an elastic material exuding from the embryo and enclosing the granulations that have become free.

Fig. 89. Posterior end of a larva seen at high magnification: *(f)* inner granular layer; *(e)* cellular outer wall striated perpendicular to its surface.

Fig. 90. Lateral portion of the same embryo.

Fig. 91. External surface of the same, brought into the focus of the objective so as to see from the front the small cells which appeared longitudinal in figures 89 and 90 *(e)*.

Fig. 92. Edge of the small disc represented in Fig. 93, Plate XVII, seen at high magnification to show its detailed structure: *(m)* cells which form its tissue; *(c)* elongated nucleus, the first rudiment of the spicules; beyond this form it is difficult to recognize them; *(d)* form already quite characteristic of the spicules; in *(g, h, i)*, these elements, becoming larger, are easy to recognize.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Histologie des larves.

Plate XVI

PLATE XVII. VERY YOUNG POLYPS BORN FROM EGGS AND STILL SIMPLE.

Fig. 93. Young oozoid forming a small disc a quarter of a millimeter in diameter attached to a Bryozoan and already colored red by perfectly characteristic sclerites, as may be seen in the following figure.

Fig. 94. Portion of the disc (Fig. 93) seen at a high magnification (500 diam.), and showing by transparency the characteristic sclerites of the Coral embedded in the tissues. This figure is only a part of the bulging disc that represents the young contracted animal.

Fig. 95. Cellular elements, granular, etc., of the same oozoid.

Fig. 96. Another oozoid more developed than the preceding one, fixed on a rock and unfolded. At its base attached debris of white foreign bodies.

Fig. 97. The same, contracted.

Fig. 98. Oozoid even more developed than the preceding ones, though simple, expanded and seen from the front.

Plate XVII

PLATE XVIII. VERY YOUNG CORAL IN THE PROCESS OF BUDDING.

Fig. 99. Oozoid (a) attached to a Thecidia showing a lateral bud *(b)*. Blastogenesis begins to develop in it.

Fig. 100. Young Coral formed by an oozoid (a) carrying a blastozooid almost as large as it *(b)*.

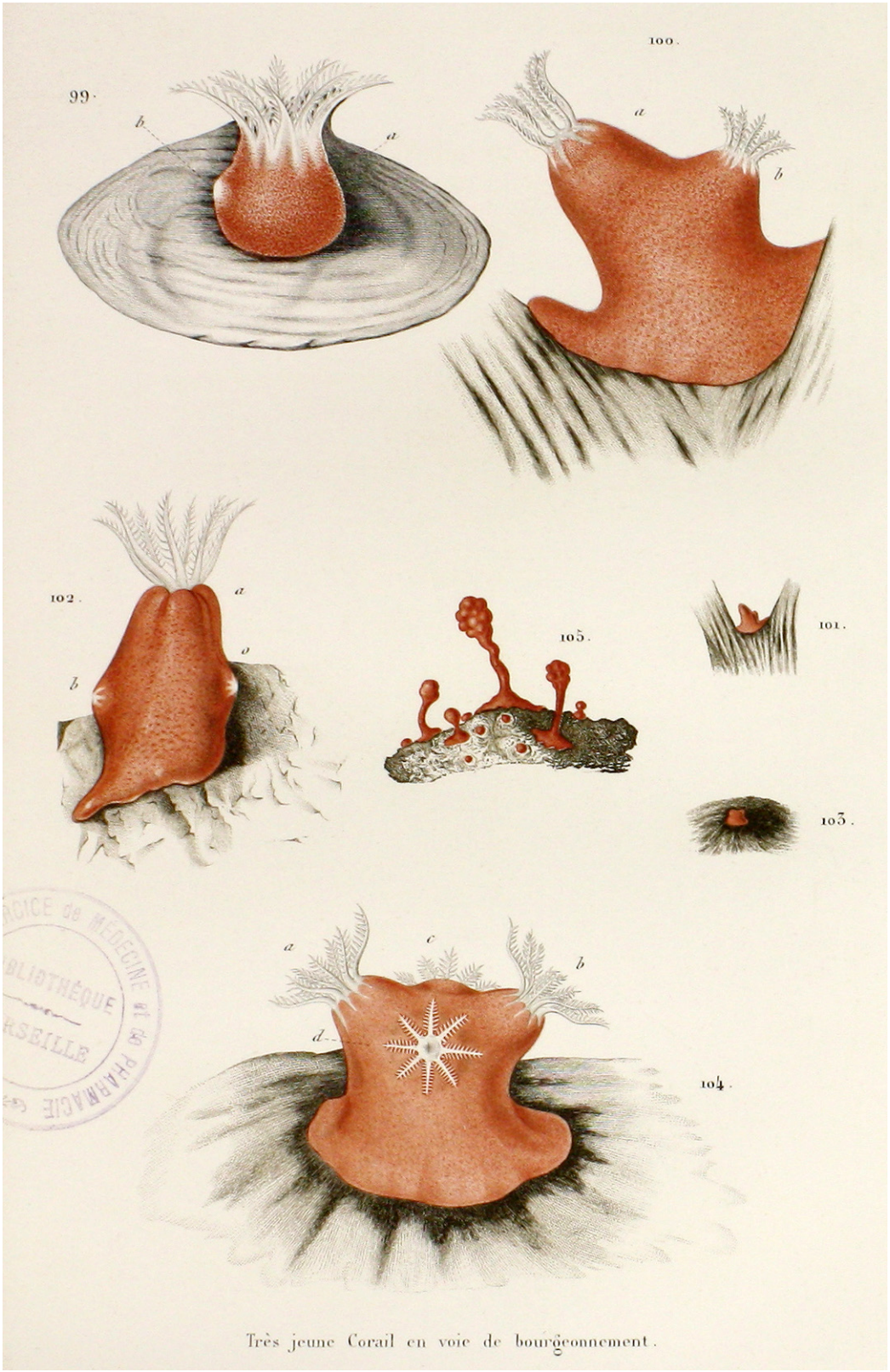
Fig. 101. Natural size of the preceding figure.

Fig. 102. Oozoid *(a)* having on its sides two blastogenetic bulges *(b, c)* that will develop into Polyps.

Fig. 103. Small zoanthodeme of natural size, enlarged in the next figure.

Fig. 104. Zoanthodeme composed of one oozoid *(a)* and three blastozooids *(b, c, d)* of different size.

Fig. 105. A small rock covered with oozoid and zoanthodemes of different sizes. The whole is of natural size.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Très jeune Corail en voie de bourgeonnement.

Plate XVIII

PLATE XIX. ORIGIN AND DEVELOPMENT OF THE AXIS.

Fig. 106. Very young zoanthodeme *(a)* attached to a life-size Bryozoan.

Fig. 107. *(b, c)* cores formed of agglomerated and fused corpuscles found in the zoanthodeme of the preceding figure and forming the starting point of the axis. Developing sclerites *(d)*, which often without being further developed are fused into the agglomerations *(b)*.

Fig. 108. Young zoanthodeme *(e)*, of natural size, more developed than the preceding one and already enclosing an axis whose form and structure are shown in the following figures.

Fig. 109. Blade with irregular and uneven edges, with thicker and more colored bands, covered here and there with small protruding corpuscles bristling with spikes: this is the beginning of the axis.

Fig. 110. Portion of the same, magnified 500 times and showing that the homogeneous tissue which joins the spicules is irregular, dotted and as if finely granulated.

Fig. 111. Small rock on which are three zoanthodemes whose polyps in *(i and j)* have been destroyed: the axes remain alone. *(j)* Blade analogous to that described in figure 109. *(i)* First form of the axis; it is very remarkable, it represents a curved blade in a horseshoe shape, irregular, formed of packets of agglomerated spicules, similar to those which I saw in figure 107. It is in the interior of the curve that the general cavity of the body of the polyp is housed, and consequently the solid blade must be found, as can be seen in *(h)*, between the external surface and the internal surface, in the middle of the coenenchyme *(g)*.

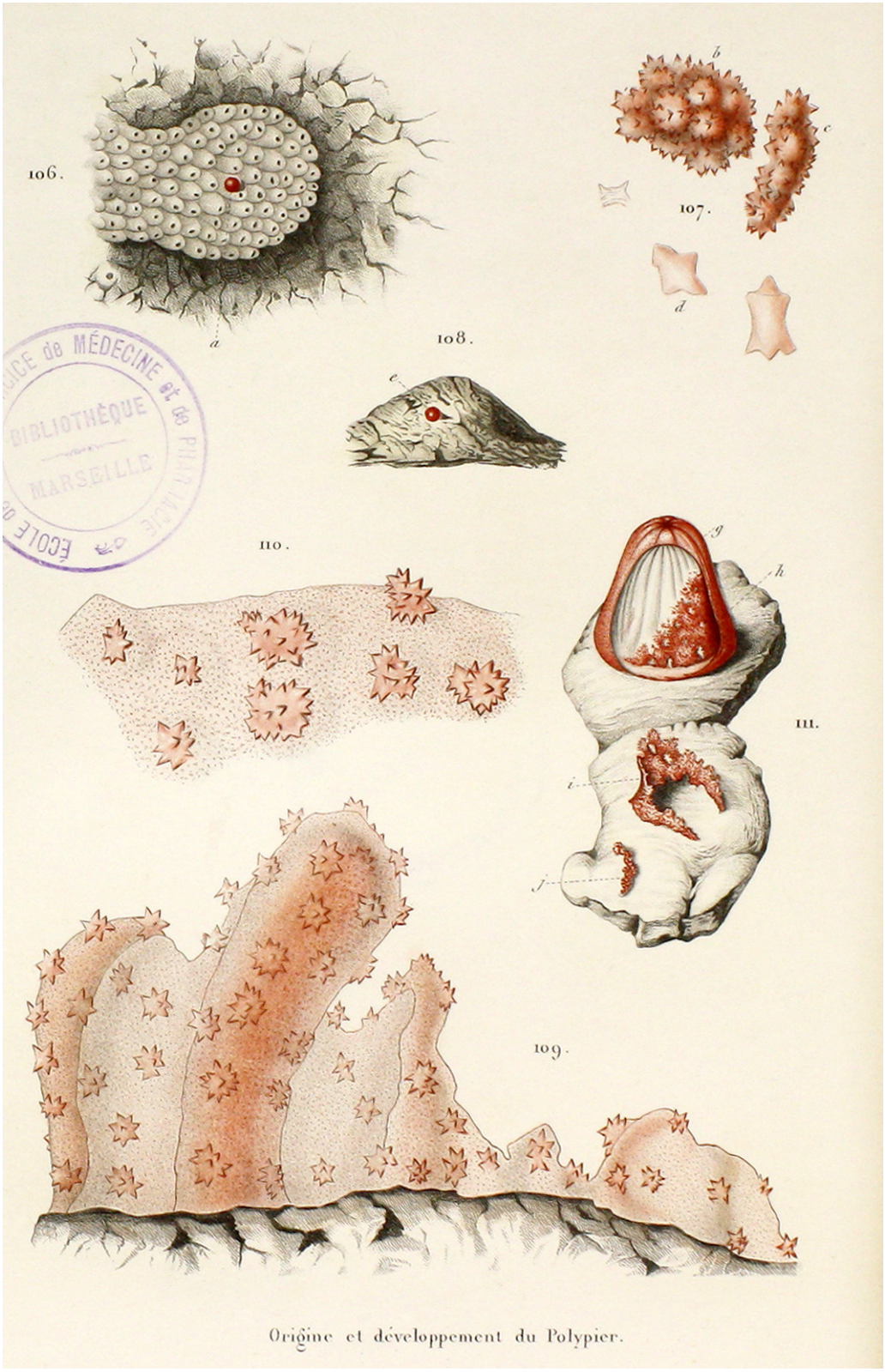


Plate XIX

PLATE XX. VARIETIES OF CORAL.

Fig. 112. Axis of the branch tip [puntarella], the drawing of which we have seen in plate l, figure 5. It is formed of three blades limiting between them dihedral angles and covered with agglomerated sclerites, protruding on its edges and faces.

Fig. 113. (a) sclerite enclosed in a cement of the same nature as it and still perfectly recognizable; *(b, c)* sclerites embedded in the cement and so well agglomerated that they hardly appear.

Fig. 114. Portion of a branch of Spanish Coral, of a very dark blood-red color and remarkable by the regular depressions that its surface presents. These are obviously calyces corresponding to the polyps of the coenenchyme; what is worthy of observation is that the striations corresponding to the canals of the coenenchyme do not exist at the bottom of these calyces. It may also be seen in this figure that it is the spaces left free between the blades of the extremity which, partitioned far and wide, form and limit these calyces *(e, d)* so exceptional and so marked.

Fig. 115. White Coral. It is a variety and not a species: its axis resembles white marble; its coenenchyme, when dead, presents a very-light yellowish tint, very well rendered in the figure.

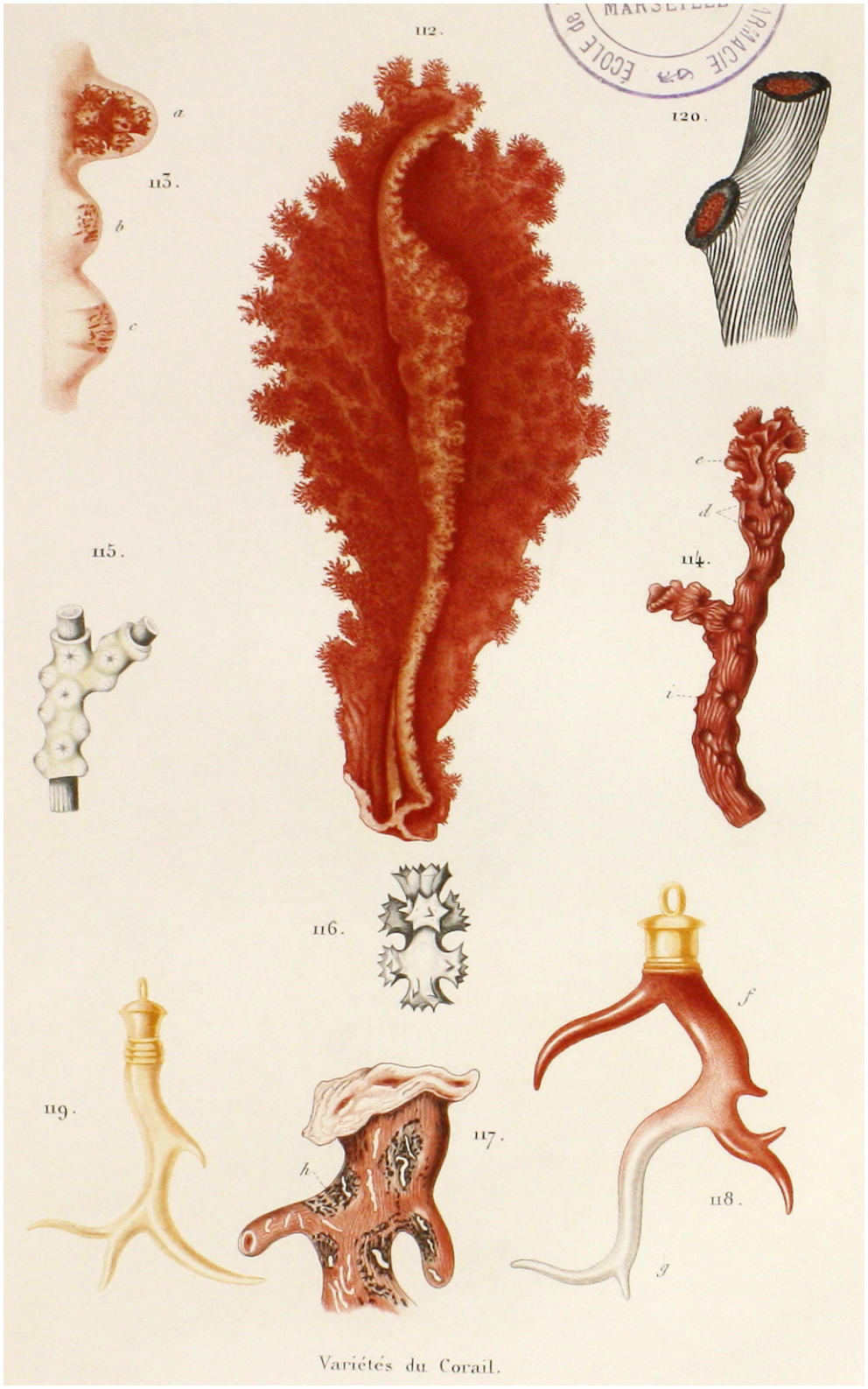
Fig. 116. A sclerite of white Coral; if we compare it with those of red Coral, Plate VI, we shall find that it is perfectly identical with them.

Fig. 117. Pink Coral, a variety known as *angel skin*, the break in the base shows patches of carmine, of the brightest pink, mingled with the purest white; this branch had been collected at sea dead, as is proved by the black and white spots on its surface.

Fig. 118. Coral jewel of a very bright red at the base *(f)*, changing to the purest white at the tip *(g)* by an insensible gradation of tone.

Fig. 119. Jewel of buff Coral.

Fig. 120. Coral blackened by a prolonged stay at the bottom of the sea; the heart is still red, the alteration having modified the color only at the surface.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Variétés du Corail.

Plate XX