



Biogenic production and their sedimentary record: a review

Luis Enrique Cruz-Guevara^a, Luis Felipe Cruz-Ceballos^b & Gladys Marcela Avendaño-Sanchez^b

^a Grupo de Investigación en Geofísica y Geología Aplicada, Universidad Industrial de Santander– UIS, Bucaramanga, Colombia. * lecruz@uis.edu.co

^b Grupo de Investigación en Geología Básica y Aplicada (GIGBA), Universidad Industrial de Santander – UIS, Guatiguará, Piedecuesta, Colombia. luisfelipecruzgeo@hotmail.com, gmas48@hotmail.com

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Abstract

The recognized biogenic production corresponds to corporal materials, and ethological structures (ichnofossils). Ethological structures include bioturbation, bioerosion, and biogenic granule-classification structures. Biogenic materials and structures traditionally include biogenic aggregates (such as fecal pellets or castings and coprolite graptolites); bioturbation structures or ichno-structures (burrows, tracks, trails, and root penetration structures); biogenic granule-classification or biostratification structures (algal and bacterial stromatolites of graded bedding of biogenic origin); bioerosion structures (borings, scrapings, and bitings); and biolithites (e.g., reef structures). This paper presents a new classification system for biogenic materials applicable to the fossil record. It summarizes our efforts to standardize terminology, use new and existing terms, correct any contradictions in some terms, and facilitate teaching and learning processes related to this subject. In our proposal, biogenic production is used for any materials or structures produced, built, modified, or used by living organisms. Biogenic production includes the following five groups: direct production (corporal, biodeposition, bioexudation, and bioencrustation materials and structures); bio-modified materials and structures (predation, bioerosion, and bioturbation); bio-built materials and structures (biofoodcaches, bioconstructions, and biostratification structures); microbial induced materials and structures; and biotools. All types of biogenic production have examples in the sedimentary record.

Keywords: sedimentology; biogenic materials; biogenic production; fossil record; nomenclature; biogenic-descriptive classifications.

Producción biogénica y su registro sedimentario: una revisión

Resumen

La producción biogénica reconocida por diferentes autores corresponde a materiales y estructuras corporales, y a las estructuras etológicas (icnofósiles). Las estructuras etológicas incluyen las estructuras de bioperturbación, las estructuras de bioerosión y las estructuras sedimentarias de bioestratificación. Tradicionalmente, las estructuras biogénicas incluyen los agregados biogénicos (tales como gránulos o castings fecales y agregados de coprolitos); estructuras de bioturbación (icnoestructuras: madrigueras, huellas, rastros, y estructuras de penetración de raíces); estructuras biogénicas de granulación o bioestratificación (estromatolitos de algas y de bacterias, laminaciones de origen biogénico); estructuras de bioerosión (perforaciones, huellas de alimentación); y biolitos (p.ej., arrecifes). Este documento presenta un nuevo sistema de clasificación de los materiales biogénicos aplicable al registro fósil. Esta propuesta resume nuestros esfuerzos para estandarizar la nomenclatura, utilizando términos nuevos y existentes, corregir cualquier contradicción en algunos términos, y facilitar los procesos de enseñanza y aprendizaje relacionados con este tópico. En nuestra propuesta, la producción biogénica se utiliza para cualquier tipo de material o estructura que los organismos producen, construyen, modifican o utilizan a lo largo de su existencia. Incluye los siguientes cinco grupos: producción directa (materiales y estructuras corporales, de biodeposición, bioexudación y bioencrustación); materiales y estructuras bio-modificados (degradación, bioerosión y bioturbación); materiales y estructuras de bioconstrucción (biofoodcaches, bioconstrucciones y sedimentos biogénicos); materiales y estructuras inducidos por microorganismos; y bioherramientas. Todos los tipos de producción biogénica tienen ejemplos en el registro sedimentario.

Palabras clave: sedimentología; materiales biogénicos; producción biogénica; registro fósil; nomenclatura; clasificaciones biogénicas-descriptivas.

1. Introduction

Organisms carry out several processes involving the production of different types of materials (shells, skeletons,

organs, tissues, body fluids, fecal, etc.). Metabolic activities of organisms that lead to the skeleton-secretion of calcium-carbonate, amorphous silica, lignin, cellulose, and phosphate. Organisms biochemically secreted most calcium-carbonate in

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sediment [1]. Most oceanic cherts' silica is probably biogenic [1]. Carbonaceous sedimentary rocks contain a substantial amount (>approx. 15 %) of highly altered remains of the soft tissue of plants and animals [2].

The fecal material of organisms, vertebrate bones, and invertebrate skeletons have phosphate concentrations. The phosphate content in feces derived from the digestion and metabolism of dietary sources and the metabolic waste products produced by cells in the body. Vertebrate bones contain a significant amount of phosphate in the form of hydroxyapatite crystals. Some invertebrate skeletons, such as those of certain mollusks, crustaceans, and other invertebrates, also contain phosphate, e.g., Masuelloids (Muellerisphaerida), planktonic zooplankton with an organic and phosphate wall, that are mostly found in deep-water oceanic sediments [3]. Trilobite skeleton, conodont tooth, and inarticulate brachiopod shells are composed of calcium-phosphate [3].

Organisms not only form sedimentary deposits and rocks directly but also transform the original texture of the sedimentary deposits to varying degrees, but it is usually that these become the dominant control on the texture of the deposits; they are simply structures that originated through the activities of organisms (named frequently as trace fossils). Organisms carry out activities during which they modify sedimentary deposits (burrowing, stirring, and mixing deposits by organisms in their search for food or shelter, e.g., bioperturbation, pelletization by organisms, etc.) and modify rocks (e.g., bioweathering, and bioerosion).

Organisms also contributed to form biostratification or biogenic granule-classification structures (algal or bacterial stromatolitic structure and homogeneous thrombolites), a mixed biogenic-sedimentological process, direct organic production-accumulation, and mechanical trapping and baffling of external particles originate them.

Furthermore, microorganisms that drive various chemical reactions, which cause the precipitation of diverse minerals and form some materials and structures, e.g., desiccation peloids [4], phosphatic nodules, etc.; we can say that many reactions that occur in sedimentary deposits are biochemical, that is, organisms drive these reactions [1]. Organisms also use materials (biotools) to carry out some vital activities. Biogenic processes, as well as inorganic processes, play an essential role in the formation of many limestones and likely play some role in the origin of chert, phosphorites, iron-rich sedimentary rocks, and, of course, carbonaceous deposits and rocks [2].

2. Biogenic production, materials, and structures

Biogenic production (BP) refers to the process of generating or producing materials, energy, or substances through biological means. BP is defined traditionally as any organic material produced by the physiologic activities of organisms, either plant or animal. Biogenic structures [2,5-8]; biogenic sedimentary structures [9]; biological processes [1]; ethological structures [10]. Biogenic structures are frequently defined as biogenically mediated, or non-biogenic deposition followed by biogenic modification [2]. Biological processes [1] include secretion of calcium-carbonate skeletons, destruction of these skeletons by predators, trapping and baffling by organisms, pelletization by organisms, burrowing and stirring by animals,

and activities of microorganisms.

Any entity product of biological activity and productivity should be considered a biogenic material or structure (BMS). BMS is used here for any materials or structures produced, built, modified, or used by living organisms. Biogenic materials include *autochthonous* and *parautochthonous assemblages* proposed by [11], and materials resulting from *taphonomic accumulation* in the sense of [12]. Biogenic production can contribute to the sedimentary record; they are considered *autochthonous* materials and form complex structures named biolithites. Biolithites [13] are mound-shaped structures built by the in-situ growth of skeleton-secreting (corporal) of sedentary invertebrate organisms, known as bioherms [1] or boundstone [14].

Autochthonous assemblages are composed of specimens derived from the local community and preserved in life position [11]. *Autochthonous* materials were not transported physically in the solid state after being accumulated or formed [15, 16]; otherwise, they were considered bioclast. Biogenic materials can also be accumulated (*parautochthonous* materials) or transported after being released and deposited (*allochthonous* materials). *Autochthonous* materials include the ecologic shell beds of [17] and exclude *allochthonous* assemblages of [11] because they are *resedimented* or *reelaborated* materials. Bioclasts are biogenic materials (e.g., skeletal, etc.) transported after their initial formation and release; bioclasts are *allochthonous* materials.

According to [2], biogenic structures include the following: (1) bioturbation structures (burrows, tracks, trails, root penetration structures); (2) biostratification structures (algal stromatolites, graded bedding of biogenic origin); (3) bioerosion structures (borings, scrapings, bitings); and (4) excrement (coprolites, such as fecal pellets or fecal castings); some authors group bioherms as well as stromatolites in bioconstructions.

The aggregates of some biogenic materials are common in the sedimentological record and have received special attention from sedimentologists using specific names, e.g., aggregates of depositional materials such as coprolites, ooids, etc.; those aggregates are called grapestones by [1,2,13], and grapestone and lumps by [18]. Grapes are materials accumulated as aggregates when formed or produce, grapes of depositional materials, e.g., coprolites, ooids, etc. They should be named grapestones when preserved in the rocks. In the case of organisms that live inside or over the sedimentary deposits and form direct aggregates of corporal material, they should be named biogenic aggregates. On the contrary, if they are aggregates by erosional-depositional segregation, the aggregates of corporal bioclast should be named bioclastic aggregates.

[19] introduced an ethological classification system for trace-maker behavior. Ethological structures are defined as the tangible evidence of the activity of one or several modern or antique organisms, which records the behavior of the producer (or producers) to a more significant or lesser extent by active interaction with an organic or inorganic substrate or by sediment production [20]. Ethological structures include biodeposition, predation, bioerosion, bioturbation, and some microbial structures. Ethological structures are classified as trace fossil structures or Ichnofossils, or Lebensspuren [1-3,19,21-27], among others. [19] recognized that similar behaviors can result in similar

morphologies of trace fossils, which can, therefore, be classified according to their ethological functions.

Trace fossils are classified into ichnogenera based on characteristics that relate to major behavioral trails of organisms and are given generic names such as *Ophiomorpha* [2]. [19] original classification of ethological structures established five major groups: resting traces (cubichnia), dwelling traces (domichnia), combined dwelling and feeding traces (fodinichnia), crawling or locomotion traces (repichnia), and combined feeding and locomotion or briefly called grazing traces (pascichnia). The organisms that produce traces are rarely preserved with the traces; thus, the trace maker is commonly not known. Therefore, the names applied to ichnogenera and ichnospecies generally do not refer to the trace makers themselves [2].

Some of these biogenic ethological structures are also designed as specific ethological classes: biodepositions as *Digestichnia* of [28,29] and bioclaustration structures as *Impedichnia* described by [30]. Icnology (ichnology) is a geological discipline that studies the ethological structures, the register of the living organism's behavior in natural supports [10].

Organisms live in relationships with others and with habitats and produce materials (BP). Biogenic production could be preserved in the sedimentary record as fossils if conditions are favorable (Fig. 1). Fossils are the evidence of past life on Earth.

In taphonomic studies, it is convenient to distinguish between biogenic production and taphogenic production, depending on whether the remains and/or signals have been generated from a biological entity of the past or formed by a pre-existing biogenic entity [15]. Currently, most specialists consider taphonomy as the study of post-release processes, e.g., decomposition, scavenging, transport, burial transformations, etc. Here, we concentrate on biogenic production and give examples of their register in the lithosphere.

Biogenic production, according to their specific origin, includes the following types (Fig. 2) [16]: materials and structures of direct production (corporal, biodeposition, bioexudation, and bioclaustration); materials and structures formed by biological modification of materials (predation, bioerosion, and bioturbation); materials and structures created and built by organisms (biofoodcaches, bioconstruction, and biogenic sedimentary structures); material used by organisms to assist themselves in some physiological activities (biotools); and finally, microbial-induced materials and structures.

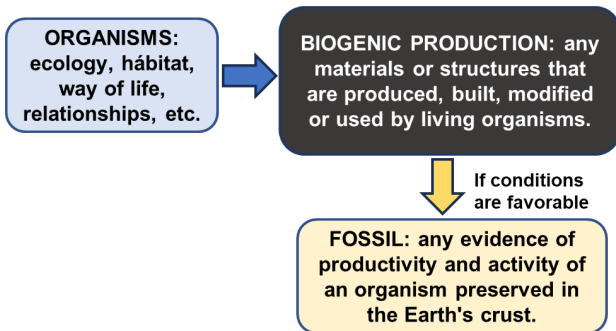


Figure 1. The relation between organisms, biogenic production, and fossils. Source: authors.

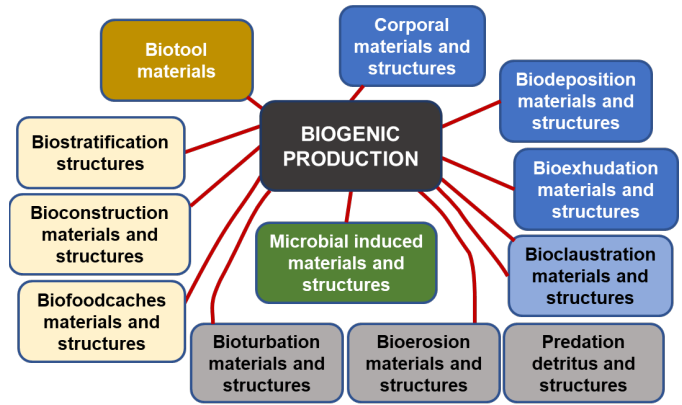


Figure 2. Biogenic production is the materials or structures produced, built, modified, or used by organisms. Blue and sky-blue box (direct production); bio-modified materials and structures (gray box); bio-built materials and structures (light yellow box); unique bio-modified-created materials and structures (green box); and biotool materials (brown box). Source: after [16].

2.1. Corporal materials and structures (CMS)

CMSs are any material made or produced by living organisms to form their bodies, including corporal biomineralized (Fig. 3 and 4), corporal soft materials, abnormal biomineralized, and retained-preserved gastrointestinal materials. *Corporal biomineralized materials and structures* (CBMS), those skeletal and relative materials formed by normal metabolism-secretion of living organisms, named bioliths and microliths, include shells, bones, eggs shell, microskeletal components (microphytoliths and microzooliths of [31-33].

CBMS with single or complex structures composed of different kinds of compounds like carbonates, amorphous silica, phosphate, etc. Organisms built corporal complex structures: bioherms, biostromes, biolithite, e.g., bryozoan-cnidarian colonies, rudists colonies, etc. CBMSs are common in the sedimentary record; some examples of well-preserved corporal entities are present in Solhofen limestone (Upper Jurassic) [34]; Orsten limestone [35,36]; and Burges Shale (Upper Cambrian) [37], among others. CMSs include reproductive materials, e.g., eggs, fruits, and seeds. A particular example of CMS are eggs preserved. Eggs are evidence of an animal's physiological processes; they are preserved inside the animal or outside it [38]. Under rare circumstances, a fossil egg may preserve the remains of the once-developing embryo inside. A wide variety of different groups of animals laid eggs that have been preserved in the fossil record since the beginning of the Paleozoic. Examples include invertebrates like ammonoids [39], as well as vertebrates like fishes, possible amphibians, dinosaurs, and reptiles [40-42].

Fruit and seed fossil assemblages exceptionally preserved of Middle Eocene Messel oil shale [43]. *Corporal soft materials* (CSM) organs, tissues, eggs, skin soft parts, and intracorporeal fluid, composed by organic compounds like nucleic acids, proteins, carbohydrates (e.g., cellulose), lignin, lipids, and resins. Corporal fluids as blood, CHONS liquid compounds as antiserum, vaccines, antigens, antitoxins, serums, and toxoids (biological production of plants [44], and gases materials (biogenic methane).

Exceptional fossil deposits that preserve soft-bodied organisms provide a rare glimpse of the true biodiversity during past periods of Earth's history [45]. Cells and soft tissues preserved in fossil bones include osteocytes, chondrocytes, blood vessels, nerve fibers, nerves, and the sheets of collagen in bone matrix [46], e.g., coelacanth fish remains [47]; soft bone material [48]; evidence of CHONS matter preserved on dinosaur cartilage [49]; mineralized belemnoid cephalic cartilage [50]; DNA record on permafrost-preserved mammoth molar [51]. Corporal materials include fossilized eggs laid or retained by animals (amniote or shell-less). *Abnormal biomineralized materials and structures* (ABMS), those minerals formed by abnormal metabolism of living organisms, include: kidney stones, e.g., bear kidney stones [52]; *urolith* of [53]; natural biogenic pearl and relatives, e.g., oysters pearl [8,54,55]; and patho-gastroliths, pathological stones formed in the stomach [56].

Retained-preserved gastrointestinal materials (RPGM), ingested or undigested food materials preserved within the digestive system, represent food items that have entered the oral cavity or gastrointestinal tract and retained within them. If gastrointestinal materials are expelled or regurgitated, they are named biodepositional materials. RPGMs include consumolite, demalite, enterolite of [53], and cololites, gastrolites, and gastroliths. *Consumolite* is a fossilized food material preserved in, or partially in, the body cavity [53]. *Demalite* is a skeletal material preserved in the body cavity of an animal that does not pertain to it [53]. *Enterolites* are fossils previously considered coprolites but interpreted to represent infilled, spiral-valved intestines [53]. Enterolite is a subcategory of cololite that originates from a spiral valve. *Cololites* introduced by [57] are fecal material preserved in the gut [58,59]. *Gastrolite* sensu [60], is a fossilized wholly or partially digested food material preserved in the stomach [53]. *Gastrolith* is a hard object of no caloric value that is, or was, retained in an animal's digestive tract [53]; because of their origin, they are considered biotools.

2.2. Biodeposition materials and structures (BDMS)

BDMSs are those ingested or undigested food materials integrated by organs and/or tissue-remains, bones, scales, feathers, and invertebrate exoskeletons voided as feces or excreted (Fig. 5), vomit, or regurgitated by living organisms. BDMS include fecal pellets [1,3,13,61], gastric pellets [62]; coprolite-like mass [63]; fecal sac [64]; gastric residues and masses with fecal materials [65]; fossilized feces of material sourced from the digestive system of organisms (bromalites) [66,67]; ejected fecal materials (coprolites and regurgitalites) [68,69]; vomit ball [70].

Coprolite is an animal's fecal material larger than 1 cm, usually elongated, sub-cylindrical to ovoid [59]. Feces produced by invertebrates are much smaller and differ in composition and shape from vertebrate coprolites [59]. Most invertebrate coprolites are in the size range of 1 mm and less in their shortest dimension, and therefore, earlier workers have suggested applying the term fecal pellets [59]. [71] numerous extant carnivorous, piscivorous, and insectivorous

species – including birds, pinnipeds, varanid lizards and crocodiles, and mammals – routinely ingest food combined with a high proportion of indigestible material that can be neither absorbed through digestion nor eliminated as fecal matter. Their solution is to egest the indigestible portion through the mouth as a gastric pellet. Emetolite was proposed for fossilized gastric pellets produced by routine emesis [71]. [66] also proposed regurgitalite as a term for all material egested through the mouth, thus replacing vomit ball in McAllister's hierarchy [70,71]. Egagrópilas, known as owl pellets, are regurgitated masses of indigestible material that owls produce after consuming their prey, e.g., owl pellets of [72]. Coprolites, cololites, and regurgitalites are collectively named bromalites [66], a term that roughly corresponds with the ethological class *Digestichnia* [28,29]. Biodeposition structures are particularly interesting to biologists, paleontologists, and educators because they provide insights into the diet, feeding habits, and ecological-palaeoecological predator-prey relationships.



Figure 3. Corporal biogenic production (bioliths). *Serpula* sp. colony in life position, autochthonous condition of *Serpula* sp. colony. *Serpula* Biolilite Limestone of Rosa Blanca Formation, Lower Hauterivian (Zapatoca, Colombia).
Source: authors.



Figure 4. Corporal biogenic production (bioliths). *Exogyra squamata* inequivalve (lateral view and life position, left; dorsal view, right). Base of the Churuvita Formation (Cenomanian), in the stratigraphic section of Sáchica Town-Samaca bridge road, Colombia.
Source: authors.



Figure 5. Biodeposition materials of depositional grapes of ovoid excrement (coprolites) of *Equus ferus caballus* (horse). Examples of fossilized grapes of coprolites are presented by different authors [28,53,59], among others.
Source: authors.

2.3. Bio-exudation materials and structures (BEMS)

BEMS are those exudation materials products of normal metabolism (silks produced by insect labial glands, e.g., spiderweb, silk cocoon or pupa), or those exudation materials products of a pathological condition that are secreted by organisms when they are injured, e.g., blood, tree resin (amber, copal), latex and relatives. Pupae are the transitional life stage between the larval and adult stages in insects undergoing complete metamorphosis, such as butterflies, moths, beetles, and flies, e.g., Holometabola are insects with pupa in their life cycle [73]. A cocoon is a protective covering spun by certain insect larvae as a part of their life cycle. It is typically made of silk, produced by specialized glands in the larval body. The primary purpose of a cocoon is to provide shelter and protection for the insect during its transformation into the adult stage. There are some evidences of bio-exudation fossils, e.g., 200 Ma leech cocoon from Antarctica [45]; Eocene fossil earthworm cocoon [74,75]; fossil record of blood [76]; amber and preserved flower [77]; dung and urine have been suggested as possible DNA sources from large herbivorous animals [78,79].

2.4. Bioclaustration structures (BCS)

BCSs are a structures formed by interaction when one organism, usually soft-bodied, embedded in a biolite substrate, e.g., the skeleton of another organism; it means biologically walled-up [80,81]. Their formation process was described originally by [82] and later in more detail by [83]. The infester must be soft-bodied, and the infester–host relationship is symbiotic, parasitic, or possibly mutualistic [80]. The resulting structures superficially resemble boring rows of subcircular pits connected by tunnels; the structure reflects the external morphology of the parasite walled-up [80]. The embedded organism can employ mechanisms to enlarge its dwelling, so the resulting cavities are of mixed origin, reflecting the interaction between occupant and host [82].

Examples of bioclaustration fossils are also presented by [84]: *Diorygma* Biernat, 1961, is a bioclaustration structure caused by an endoparasitic or commensal worm on Devonian atrypid brachiopods [84]; the small spiral bioclaustration structures *Helicosalpinx* Oekentorp (1969) (Devonian); *Torquaysalpinx* Ptusquellec 1968 (Devonian) [84]; and *Catellocaula vallata* [80]. These structures have been gathered into an ethological group called Impedichnia [30] because the infester operates as a limiting factor to the growth of the host; some holes traditionally ascribed to boring show distribution and morphologies more in keeping with claustration structures [82].

2.5. Predation detritus and structures (PDS)

PDS correspond to those aggregates of corporal detritus produced by predation-disarticulation-fragmentation of previously formed corporal entities (skeletons, tissue, etc.). PDS of accumulated predation-detritus, including gravel, sand, and mud-size materials. Predation is a common ecological interaction where one organism, known as the predator, captures and feeds on another organism, called the prey. Predation is a fundamental aspect of many ecosystems and

plays a vital role in regulating populations and shaping community dynamics. Predators have evolved adaptations such as sharp teeth, claws, speed, camouflage, or venom to effectively capture and subdue their prey. Prey organisms, on the other hand, have developed defensive mechanisms like camouflage, spines, toxins, or alarm calls to avoid or deter predation.

Predation is widespread across the animal kingdom. For example, lions predate zebras and antelopes, wolves prey on deer and rabbits, and hawks hunt smaller birds or rodents. However, predation is not limited to carnivores. Some herbivores, such as certain species of insects or birds, may also engage in predation by feeding on other animals, often to supplement their diet with additional nutrients. When organisms prey on others and consume them, they commonly generate remains and deposits that include the fragmented parts of the prey, e.g., when predators consume hard-shelled prey, they often break or fracture the shells to access the soft tissues inside. Predation processes are described as the degradation of calcium-carbonate skeletons into skeletal debris [1]. In certain predator-prey interactions, predators may consume their prey in specific locations, leaving evidence of the kill. These sites can accumulate fragments of bones, fur, feathers, or other remains because of repeated predation events, e.g., caves and rock shelters were the final destination of the food transport trajectories of humans and other predators [85-88].

Deposits formed by predation are described also as faunal accumulations [89]; and shell-crushing accumulation by durophagous and opportunistic-generalists, most probably fishes [90]. Predation also creates structures and traces made by organisms engaging in durophagy, performed on hard-shelled materials (holes, scratch, feeding traces, etc.), or structures made by organisms in bones while depredating (feeding or predation traces), e.g., bite marks caused by fish [91]; termite boring on woods [92]; drill hole attributed to gastropod predation [93]; lineated perforation by mosasaur predation [94]. These predation traces and structures are included in bioerosion structures.

2.6. Bioerosion structures (BES)

BES are structures excavated mechanically or biochemically by an organism into a rigid inorganic substrate [5]. Those special structures product of the destruction of consolidated (hard) substrates, inert substrates [95]. Bioerosion term was proposed by [96]. Bioerosion structures made on inert consolidated substrates are ethological structures as well as sedimentary structures [20]. BES include bioerosion made on hard parts of the anatomy of living organisms of [20] (borings, scrapings, and bitings). Some predators, such as certain snails or predatory gastropods, have specialized radulae (rasping tongues) or radular teeth that they use to drill holes through the shells of their prey.

Marine organisms like boring sponges, bivalves (e.g., shipworms), or polychaete worms can create these burrows and tunnels as they feed on or inhabit the hard shells of other organisms. BES also includes scratch marks of [52] made by organism's claws in some materials like wood or rocks when delimiting territories (delimiting traces); and Bärenschliffe (animal polished rock surfaces) are smooth, polished, and often

shining surfaces, thought to be caused by passing bears or other animals rubbing their fur along the walls [52]. These structures and traces created by organisms engaging in durophagy provide essential evidence for understanding past predator-prey interactions, ecological relationships, and the adaptations of predators to consume hard-shelled prey. BES offers valuable insights into the behaviors, feeding strategies, and evolution of organisms involved in predation. See the interaction organisms with hard substrate [97]. Bioerosional marine trace fossils catalogue is presented by [84].

2.7. Bioturbation materials and structures (BTMS)

BTMS include biogenic sedimentary structures of [5]; nonbiogenic deposition followed by biogenic modification [2]. BTMS are part of ethological structures [10]. BTMS formed by biological reworking include remobilization-reorientation, mixing and segregation of previously formed sedimentary deposit [98]. Those that involve distortion and/or destruction by organisms of the arrangement and/or stratification of unconsolidated substrates [20]. Crawling, resting, and dwelling activities making by living animals or plants, include among others: footprints, tracks, borings, burrows (Fig. 6), root penetration structures [99], nest insect larvae [100]; icnite with print skin [101,102], among others.

Burrows are tunnels or holes in the ground created by certain animals for various purposes, such as shelter, nesting, protection from predators, foraging, reproduction, or hibernation-thermoregulation. Burrowing behavior is widespread among invertebrates and vertebrates, and different species have evolved various burrowing strategies based on their ecological needs and habitats. Examples of animals known for creating burrows include rabbits, badgers, foxes, groundhogs, and a lot of invertebrates. Tracks are features produce over de loose materials or cooling lavas (named icnites when fossils), e.g., track left by the tail of a reptiles, footprints; bear footprints preserved in volcanic ashes [103]; etc. Borings are bioperforation, they are part of burrows.

Bioturbation structures include also microbial peloids of [4,19], and microbially induced sedimentary structures [104,105], materials described and included after in the text. Bioturbation also produces bio-detritus waste dumps (BDWD). Animal activity produces debris dumps when they build their galleries and throw the excess material outside (see Fig. 7). BDWD includes bio-depositional excavation dumps and pellets, pseudo-feces, filings, and other residues of bio-erosive activity of [10], not fecal or regurgitalites. BDWD includes pseudo-feces and fecal castings [2,106-108].

Burrows, track-sand boring are present in the sedimentological record, e.g., spiral burrows of rodents [21]; vertebrate footprint [24]; fossil worm burrows [109], among others. Contrasting textures of discontinuous burrows created by bioturbation of sediments (e.g., microorganisms, fungi and worms' burrows) are designed as burrow-mottled sediments or mottled structures [1,110]. Mottled structures are a general term describing an irregular, splotchy arrangement of two contrasting kind of sediments, with different colors (gray and light green), create by effects of bioturbation in which the infilling of borrows create discontinuous structures [1].



Figure 6. *Thalassinoids*, horizontal ramified to T-branched box-works, mazes, and shafts, unlined and unornamented. Arenisca Dura Formation, Upper Cretaceous, Iza, Colombia.
Source: authors.

The study of bioturbation is essential in understanding the interactions between organisms and their environment, as well as the ecological functions they provide within ecosystems. Moreover, the presence and characteristics of burrows in sedimentary rocks can provide valuable information about past environmental conditions and the behaviors of ancient species. More information about bioturbation structures and ichnofossils see [5,10,26,111-114], among others.

2.8. Biofoodcaches materials and structures (BFMS)

BFMS are those buried and stored food by organisms throughout the year in nests or even pressed into the bark of trees or in the soil, e.g., surplus food, bones, and pollen. Animals engage in food caching as a survival strategy, particularly in environments where food availability fluctuates or where they need to prepare for periods of scarcity, such as winter or during migration. These animals, by creating food caches, can ensure a steady food supply when resources become limited; this behavior is observed in various species, including mammals, birds, and insects.

Honeybees store nectar, squirrels' stock up nuts, ants collect plant detritus, dogs bury bones, bird gather fruits, etc. The food caches process involves collection, transportation, hiding or burial and retrieval. The investigation of fossils food caches can shed light on the paleo-vegetation and paleofauna as well as on various aspects of the paleoecology and paleoclimate [115]. Fossil foodcaches are rare in the geological record [115]. Geologically oldest examples of food hoarding [116-118]. Examples of BFMS fossilized are: Miocene *Celtis* silicified tree stump with burrow filled and an accumulation of *Carya* nuts by Kangaroo-rat heteromyid [119]; Miocene nut cache in dunes [115].

2.9. Bioconstruction materials and structures (BCMS)

BCMS refers to constructions produced by living organisms (plants, animals, and microorganisms). Organisms make structures or habitats through natural activities to house

embryos or live in (Fig. 8). Bioconstructions are structures made by secreting skeletons and corporal entities, and construction uses external materials. Bioconstructions include colonies of tiny organisms (e.g., cnidarians or bryozoans' polyps) that secrete calcium carbonate skeletons, growing closely together and forming complex structures, e.g., reef.

Also, plants form forests, a large area dominated by trees and other woody vegetation. Forests are incredibly biodiverse ecosystems, providing habitats for various plants, animals, fungi, and microorganisms. They often support complex food webs and interactions among different species. Other organisms made bioconstructions using external materials to build dwelling and nest structures, e.g., wasp nests, beehives, termite mounds, vertebrate nests, etc.

Bioconstruction includes *coprinisphaera* (necrophagous dung beetle nest), those materials produced by reworking, transport, and use of fecal excrement materials for nest proposes [120]. These natural constructions benefit the organisms that create them and have ecological implications, as they can



Figure 7. Biodetritus waste-dumps (BDWD) are loose materials removed during the maintenance and cleaning of their shelter. A) BDWD by ants with entrance and ventilation shaft (arrow) to the shelter galleries of the colony. B) Earthworm (*Lumbricus terrestris*) castings (mud pancakes) consist of a mix of earthworm fecal matter and detritus (Piedecuesta, Colombia). Fossil evidence of BDWD is presented in [106,107,108], among others.
Source: authors.

influence habitats, nutrient cycling, and ecosystem dynamics. Some examples of fossilized bioconstruction are trilobite nests [121], ant nests [122], fossil bee nests [123], Jurassic termite nests [124], dinosaur nests [125], among others.

2.10. Biostratification structures (BS)

BSs are produced by trapping and baffling fine materials (sand, silt, and clay) by organisms; they are biogenically mediated structures. BSs include algal stromatolites by trapping and baffling [1] and biomechanical sedimentation [126]. Microorganisms carry out the biological process of trapping and sifting sedimentary materials (bioaccumulation and sedimentation). Shallow water filamentous blue-green algae, mats of leaves containing sticky organic matter (mucilage), trap fine-grained foreign particles, forming a sheet with them; the alga forms another mat that again traps foreign materials, also they intercalate sedimentary materials of diverse origin with their materials (CaCO₃ algal plates). Among the sedimentary materials trapped, it can also find diatoms, fungi, crustaceans, insects, spores, pollen, rhodophytes, and abiogenic materials are also trapped.

Algal stromatolites have many shapes, including domed cabbage heads (hemispherical) with finely irregular laminations. Stromatolites date back to the Precambrian, were common throughout the Phanerozoic, and are known from modern environments where carbonate materials are present [1,2]. Some examples of BSS are algal Proterozoic stromatolites [127], and Recent subtidal stromatolites [128,129]. Stromatolites have played a crucial role in shaping Earth's history; they represent some of the earliest evidence of life on Earth and played a significant role in the development of Earth's atmosphere. Studying stromatolites provides valuable insights into the ancient environments in which they formed. The structure and composition of stromatolites can reveal information about ancient sea levels, water chemistry, and sedimentary environments [130]. Not all geologists regard biostratification structures as trace fossils, which are not commonly included in published discussions of trace fossils [2].

2.11. Biotool materials and structures (BTMS)

BTMS refer to external materials used by living organisms to assist themselves in some physiological activities or manipulated to perform a specific function or task. Include ingestion of organic-rich clays, clays, salts, and rock fragments (e.g., stomach stone or gastrolith). Gastroliths, stomach stones, are rock fragments held inside a gastrointestinal tract, or retained in the muscular gizzard and used to grind food [53,56,131-133]. Aquatic animals, such as plesiosaurs, may have used them as ballast, to help balance themselves or to decrease their buoyancy [134]. Certain crayfish store gastroliths in their stomachs. Especially crayfish living in freshwater store these gastroliths as the presence of calcium is limited in freshwater, these gastroliths serve as a calcium source for molting [135]. Examples of biotool structures conserved as fossils include gastroliths from sauropods [133]; stomach stones in marine tetrapods [134]; among others.



Figure 8. Bioconstruction samples. A) The wasp nest of *Polistes* (Zapatoca, Colombia) comprises chewed plant fibers and saliva. B) Bird nest, made up of fibers of plant detritus, feathers, and other materials. Examples of fossilized bioconstruction are presented in [121,122,123,124,125], among others. Source: authors.

2.12. Microbial induced sedimentary materials and structures (MISM and MISS) [104,136]

There are numerous kinds of structures formed by mediation of microbes (Fig. 9), e.g., microbialite, helictites, etc., [104,105,137,138]; microbial peloids [4]; embryo fossilization [139]; and microbially induced sedimentary structures [104,105]. Microbially induced sedimentary structures are not considered as traces and neither are structures resulting from bioclasturation [140].

Microbialite is a generic name for the benthic sedimentary materials and deposits of mineral-microcrystalline (diameter <16 µm) formed with the mediation of microbes by accretion-coated or mineral precipitation-accumulation initially proposed by [141]. Being formed in situ, a microbialite can be seen as a type of boundstone where builders are microbes, and the precipitation-accumulation of carbonate is biotically induced instead of forming tests, shells, or skeletons. Microbialites can also be defined as microbial mats [142], and biofilms by [143]. Bacteria can precipitate carbonate both in shallow (e.g., cyanobacteria) and deep water so that microbialites can form regardless of the sunlight [144-146].

MISS includes the following specific types: microbial mediated cave structures (biofilms), microbial-desiccation materials and structures, microbial induced minerals, coated microbial materials and structures, and microbial-induced gases.

Microbial mediated cave structures (biofilms), microbial mediation of complex subterranean mineral structures of [137], e.g., *Helictites* a speleothem (tubular-irregular cave-formed structure) found in a limestone cave that changes its axis from the vertical at one or more stages during its growth, more information in [137].

Microbial-desiccation materials and structures, those formed by microbial activity and desiccation-weathering process of materials during eodiagenetic process, named bioweathering peloids (weathering peloids or diagenetic intraclast according to [4]).

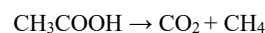
Microbial induced minerals (MIM), those crystals and minerals formed by activities of microorganisms that drive various chemical reactions, e.g., bacteria-induced mineral precipitation [1,147,148]. MIMs are also formed by biodegradation. Biodegradation is the decay or breakdown of materials that occurs when microorganisms (bacteria and fungi) use organic and inorganic materials as a source of nutrients (carbon, nitrogen, oxygen, etc.) that give them the energy to carry out their vital processes, e.g., biodegradation of basalt rock [149]; bacterial degradation of gypsum, and calcite formation [1]. These processes assist the precipitation of diverse minerals, including calcite, native sulphur, and pyrite [1,147]; siliceous sinter, geysirite, and silica scale originate by microbial silica deposition in geothermal hot waters [150]; precipitation of low-temperature dolomite from an anaerobic microbial consortium [151,152]; emerging saturated karst waters may precipitate calcite, often under biogenic mediation, to form sometimes extensive deposits of tufa or travertine, such as those of Plitvice, Croatia [3]; and microbially mediated formation of Fe-carbonate minerals under extreme acidic conditions [138].

Coated microbial materials and structures (CMMS) are those formed or grown in place by a mixed chemical coated-biogenic (microbial) process or biochemical precipitation of concentric coating of microcrystalline carbonate. CMMS form in warm,

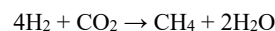
supersaturated, shallow, and highly agitated marine water intertidal environments. CMMS are materials accumulated alone or forming aggregates and are not transported physically as solid objects after their formation, e.g., ooids, algal pisolites, rhodoliths, and microbial polymetallic nodules (ferromanganese nodules). CMMSs exclude diagenetic nodules. Ooids and algal pisolites are described by [1] and as oolites by [13]. Rhodoliths by [153] and [154]. Microbial communities of the ferromanganese nodules by [155].

Microbial-induced gases, e.g., organisms directly produce methane as products of digestive processes by bacteria. Methane (CH₄) is a natural product of the digestive processes by certain microorganisms, particularly methanogenic archaea. Methane is found in the gastrointestinal tracts of several animals, including ruminants (such as cows and sheep) and other herbivores. During anaerobic digestion, bacteria and archaea break down the organic matter in the absence of oxygen, producing methane gas as a metabolic product. The methane gas is then released from the animal's digestive system through burping (eructation) and flatulence (farting).

Methane in the atmosphere has a concentration of 1.7 ppm (vol.) and is dominantly formed by biological processes [3]; biogenic methane is a biogenically mediated material. Biogenic methane in natural environments is generated by several natural processes involving aerobic (oxygen-containing) and anaerobic (oxygen-deprived) microorganisms. In the deepest, most reducing environments, methane may be produced by the actions of methanogenic bacteria using two main pathways [3]:



Alternatively,



Methane produced in this fashion may seep back into seawater to be re-oxidized to CO₂ or may be stored temporarily for thousands to millions of years as the volatile methane clathrate [3]. Methane (CH₄) is a potent greenhouse gas, and its presence in the atmosphere has significant implications for climate change. Biogenic methane is vital in the global carbon cycle and atmospheric composition. It is part of a complex interplay between methane sources and sinks, where "sinks"

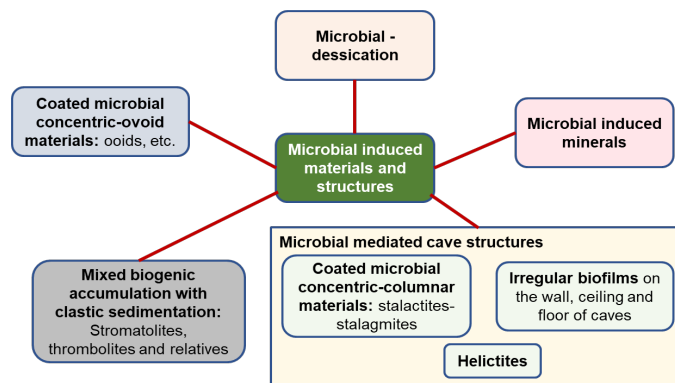


Figure 9. Microbial-induced materials and structures. *Microbialite* is a generic name for the benthic sedimentary materials and deposits of mineral-microcrystalline (diameter <16 µm) formed with the mediation of microbes by accretion-coated or precipitation-accumulation.

Source: authors.

refer to processes that remove methane from the atmosphere. Some of the significant methane sinks include chemical reactions in the atmosphere and its oxidation by certain bacteria. While biogenic methane is a natural component of the Earth's carbon cycle, human activities can influence its production and release. For instance, deforestation, land-use changes, and increased agricultural practices can alter the balance of methane emissions from various sources. Changes in the distribution and abundance of wetlands due to climate change can also impact biogenic methane emissions.

3. Conclusions

Biogenic production corresponds to all materials and structures produced, built, modified, or used by living organisms.

Biogenic production includes the following five groups: directly production (corporal, biodeposition, bioexudation, and bioclastration materials and structures); bio-modified materials and structures (predation, bioerosion, and bioturbation); bio-built materials and structures (biofoodcaches, bioconstructions, and biogenic sedimentary); unique modified-created materials and structures (microbial induced materials and structures); and bio-used materials (biotools).

Corporal materials include biomineralized normal (skeletons) and abnormal (kidney stones and biogenic pearl), retained-preserved gastrointestinal materials, and soft materials (organs, tissues, and fluids).

Biodepositional materials include ejected fecal materials (coprolites and regurgitalites).

Bioexudation materials include silks produced by insect labial glands and exudation materials from a pathological condition, e.g., amber, copal, latex, etc.

Bioclastration or soft-bodied embedded in a biolite substrate.

Predation structures are aggregates of corporal detritus produced by predation-disarticulation-fragmentation of previously formed corporal entities, e.g., skeletons, tissue, etc.

Bioerosion structures include bio-perforation made on hard parts of the anatomy of living organisms. Also, include scratch marks made by organism's claws in some materials like wood or rocks when delimiting territories (delimiting traces); and Bärenschliffe (polished rock surfaces by animals) smooth, polished, and often shining surfaces, thought to be caused by passing bears or other animals, rubbing their fur along the walls.

Bioturbation structures include footprints, tracks, borings, burrows, root penetration structures, and biodeposit waste-dumps.

Biofoodcaches are structures formed from buried and stored food by organisms.

Bioconstruction includes structures made by directly secreting skeletons and corporal materials (e.g., reef, forest) and construction made using external materials, e.g., wasp nests, beehives, termite mounds, and vertebrate nests.

Biostratification structures are produced by trapping and baffling fine materials (sand, silt, and clay) by organisms; they are biogenically mediated structures, e.g., stromatolites.

Biotools are external materials living organisms use to assist themselves in some physiological activities or manipulate to perform a specific function or task, e.g., gastroliths.

Microbial-induced materials and structures include microbial desiccation, microbial-induced minerals, microbial-mediated cave structures, coated microbial concentric-ovoid, and microbial-induced gases.

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Conflicts of interest

The authors declare that there are no conflicts of interest associated with this work.

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L.E. Cruz-Guevara, is BSc. in Geologist, in 1983 from the Universidad Nacional de Colombia, MSc. and Dr. in Geology in 2008, from the UZ, Spain. Is titular professor since 1984, of Paleontology, Sedimentology, and field Geology of sedimentary rocks at the Universidad Industrial de Santander – UIS, Colombia. ORCID: 0000-0002-8345-4870.

L.F. Cruz-Ceballos, is BSc. in Geologist in 2017 and MSc in 2019, all of them from the Universidad Industrial de Santander – UIS, Colombia. Junior researcher sedimentology and organic geochemical. MSc Software developer in 2004, from the Andes University, Bogota. Colombia. Software senior developer. ORCID: 0000-0002-4339-2302.

G.M. Avendaño-Sánchez, is BSc. in Geologist in 2017 and MSc in 2019, all of them from the Universidad Industrial de Santander – UIS, Colombia. Junior researcher sedimentology and organic geochemical. Software junior developer since 2023. ORCID: 0000-0001-8215-5863.