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Echinoderm ichnology: bioturbation, bioerosion and related processes

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Abstract.—Among invertebrates and both in modern and ancient marine environments, certain echinoderms have been and are some of the most active and widespread bioturbators and bioeroders. Bioturbation and/or bioerosion of regular and irregular echinoids, starfish, brittle stars, sea cucumbers and crinoids are known from modern settings, and some of the resulting traces have their counterparts in the fossil record. By contrast, surficial trails or trackways produced by other modern echinoderms, e.g., sand dollars, exhibit a lower preservation rate and have not yet been identified in the fossil record. In addition, the unique features of the echinoderm skeleton (e.g., composition, rapid growth, multi-element architecture, etc.) may promote the production of related traces produced by the reutilization of echinoderm ossicles (e.g., burrow lining), predation (e.g., borings), or parasitism (e.g., swellings or cysts). Finally, the skeletal robustness of some echinoids may promote their post mortum use as benthic islands for the settlement of hard-substrate dwellers.

Introduction

By means of trace fossils, ichnology studies the evidence of inter-actions between organisms and substrates as a result of their life activity in the geological past. Therefore, ichnology is part of paleoecological analysis, which can be defined as the study of at least one of the three possible pairs of relationships established in ecosystems: (1) interaction between taxa, (2) influence of taxa on the environment, and/or (3) influence of the environment over the taxa.

Trace fossils are the biogenic structures (also called ethological structures) that record the activity of organisms in the geologic past, and are divided into three broad categories: (1) biogenic sedimentary structures, (2) bioerosion structures, and (3) other evidence of activity. The biogenic sedimentary structures are those produced by the activity of organisms on or in unconsolidated substrates. They include bioturbation structures (e.g., burrows, trails, footprints), and evidence of biodeposition (e.g., coprolites, fecal pellets) and biostratification (e.g., microbial mats). The bioerosion structures originate by mechanical and/or chemical biological activity on hard inorganic (rock) or organic (woody, calcareous or phosphatic skeletons) substrates. Structures such as eggshells, cobwebs, etc. fit in the catchall of other evidences. Seilacher (1953) proposed a classification system of trace fossils based on the reflected behavior. From this first proposal to the present, numerous additions and refinements to the initial scheme have been suggested. Such proliferation complicates an effective classification since many traces are the result of several simultaneous or successive behaviors (see Vallon et al., 2016 and references therein).

Our study has involved the compilation of available infor-mation on traces made by, received by, or directly related to echinoderms, from the Cambrian to the Recent. The highly diverse echinoderms can be common in the fossil record in various marine environments, which has facilitated their use in numerous paleobiological studies. In parallel, their ichnological record may be composed of both direct and indirect evidence: (1) direct evidence corresponding to the bioturbation and bioerosion structures resulting from the different burrowing and boring behaviors that may be conducted by many groups of echinoderms (mainly echinoids, asteroids, ophiuroids and holothurians); and by contrast, (2) indirect evidence, not directly produced by echinoderms as such, but produced in or on their skeletons (syn-vivo or post-mortem interactions) or, at least, in or on some of their component skeletal elements. These, mainly consist of traces related to predation or symbiotic relationships with various other organisms and even to the exploitation of their skeletons, ossicles and/or spines to construct burrow linings or domiciles.

The following sections constitute an extensive review of the present-day knowledge on the modern and fossil record of ichnologic structures related to echinoderms. The high ichnodiversity of echinoderm-related traces is tracked along the geological record. This allows the fidelity of the traces to be followed and records the potential ecological behavior of the echinoderm taxa in different geological periods.

Modern and fossil echinoderm ichnological record

Among both fossil and modern echinoderms, there are active and significant burrowers and borers (mainly echinoids, but also asteroids, ophiuroids, holothurians and crinoids); consequently, their burrowing and boring behaviors have a high potential to

produce an extensive ichnological record (Fig. 1). To date, 22 ichnogenera have been erected (leaving aside ichnotaxonomic discussions; see Table 1), which correspond to bioturbation and bioerosion structures attributable to echinoderms.

Echinoid bioturbation structures.—Among bioturbation structures attributed to the burrowing activity of echinoderms, the ichnogenera *Scolicia* De Quatrefages, 1849 and *Bichordites* Plaziat and Mahmoudi, 1988 are the most common and best known, since the Jurassic and the Oligocene respectively. They consist of large horizontal to subhorizontal, meandering, meniscate backfill burrows bearing one or two drains respectively (Figs. 1.12–1.14, 2.1–2.4) (e.g., Bromley and Asgaard,

1975; Uchman, 1995; Bromley et al., 1997; Gibert and Goldring, 2007, 2008; Seilacher, 2007; Bernardi et al., 2010; Caruso and Monaco, 2015).

Detailed neoichnological studies, both from aquaria and natural environments, have shown that these large meniscate traces result from the backfilling activity of spatangoid echinoids ploughing through the sediment (e.g., Kanazawa, 1992, 1995; Bromley et al., 1997); although the older spatangoids date back to the Early Cretaceous (Villier et al., 2004), this backfilling activity is known from the Tithonian (Late Jurassic; Tchoumatchenco and Uchman, 2001). The occurrence of one or two drains (i.e., cylindrical tubes constructed to conduct water away from the burrow) is related
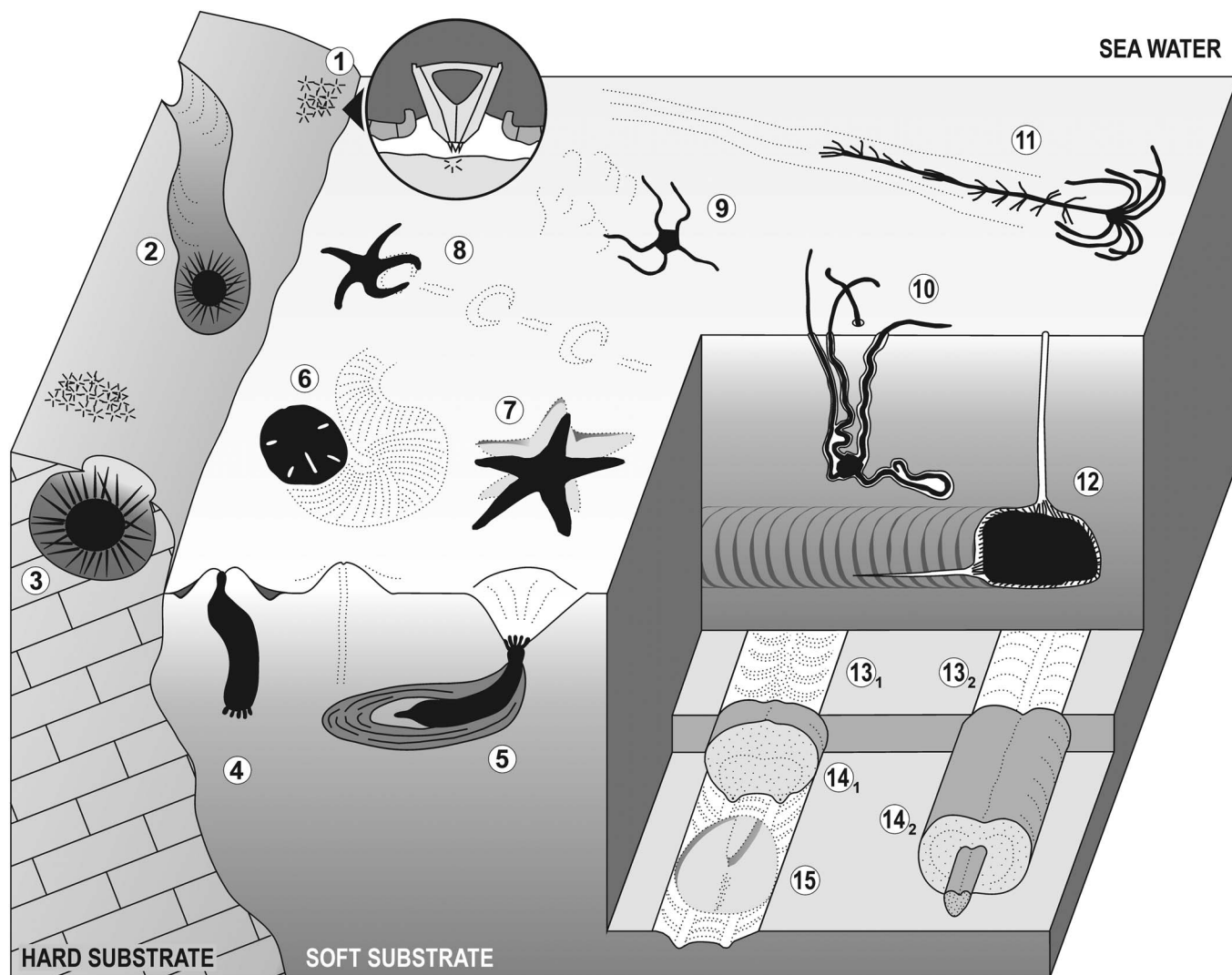

Figure 1. Diagram showing bioturbation and bioerosion of the main groups of extant echinoderms. Regular echinoid bioerosion: **(1)** bite traces (*Gnatichnus*-like) produced by grazing on hard substrates (detail of the Aristotle's lantern within the circle); **(2)** long and continuous grooves (*Ericichnus*-like) attributed to a pascichnial/agrichnial or domichnial behavior; and **(3)** circular pits (*Circolites*-like) used as more or less permanent domiciles. Holothurian bioturbation: **(4)** simple vertical shaft and **(5)** thickly laminated burrow (*Artichnus*-like) produced by molpadid holothurians (modified from Ayranci and Dashtgard, 2013). Irregular echinoid bioturbation: **(6)** surficial and meniscate locomotion trace produced by the sand dollar *Mellita quinquiesperforata*. Asterozoan bioturbation: **(7)** sea star resting trace (*Asteriacites*-like); **(8)** sea star locomotion trace (*Arcichnus*-like; modified from Sutcliffe, 1997); **(9)** ophiuroid locomotion trace (*Ophioichnus*-like; modified from Bell, 2004); and **(10)** burrow produced by the brittlestar *Hemipholis elongata* (modified from Christensen and Colacino, 2000). Crinoid bioturbation: **(11)** locomotion trace of the isocrinid *Neocrinus decorus* (*Krinodromos*-like; modified from Baumiller and Messing, 2007). Irregular echinoid bioturbation: **(12)** spatangoid ploughing through the sediment (modified from Gibert and Goldring, 2008); **(13)** horizontal biserial menisci (*Laminites*-preservation; modified from Uchman, 1995); **(14)** subhorizontal, meandering, meniscate backfill burrows bearing one (14.2; *Bichordites*-like) or two (14.1; *Scolicia*-like) drains (modified from Uchman, 1995); and **(15)** spatangoid resting trace (*Cardioichnus*-like; modified from Smith and Crimes, 1983). Depicted echinoderms are not to scale.

Table 1. Ichnotaxa ascribed to echinoderm bioturbation or bioerosion. S.R.: Stratigraphic range; Etho.: Ethology; *: type ichnospecies. [1] sensu Uchman (1995); [2] sensu Radwanska (1999); [3] sensu Schlirf (2012); [4] sensu Knaust and Neumann (2016); [5] sensu Mángano et al. (1999). Stratigraphic Range: Cam., Cambrian; E.D., Early Devonian; L.Car., late Carboniferous; T., Triassic; M.T., Middle Triassic; J., Jurassic; M.J., Middle Jurassic; E.K., Early Cretaceous; L.K., Late Cretaceous; E., Eocene; Oli., Oligocene; M., Miocene; L.M., late Miocene; E.Plio., early Pliocene; t., today. Ethology: AGR, Agrichnia; CUB, Cubichnia; Do, Domichnia; FOD, Fodinichnia; MOR, Mortichnia; PAS, Pascichnia; REP, Repichnia.

		Ichnogenus	Ichnospecies	Ichnotaxonomic status	S. R.	Etho.
ECHINOID TRACES	Bioturbation	*Bichordites* Plaziat and Mahmoudi, 1988	*B. monastiriensis* * Plaziat and Mahmoudi, 1988		Oli. / t.	PAS
			B. kuzunensis Démircan and Uchman, 2012		" "	" "
		Cardioichnus Smith and Crimes, 1983	*C. planus* * Smith and Crimes, 1983		L.K. / E.Plio.	CUB
			C. ovalis Smith and Crimes, 1983		" "	" "
			C. foradadensis Plaziat and Mahmoudi, 1988		" "	" "
			C. reniformis Mayoral and Muñiz, 2001		" "	" "
		Scolicia de Quatrefages, 1849	*S. prisca* * de Quatrefages, 1849		Cam. / t.	PAS
			S. strozzii (Savi and Meneghini,1850)		" "	" "
			S. plana Książkiewicz, 1970		" "	" "
			S. vertebralis Książkiewicz, 1977		" "	" "
		Laminites Ghent and Henderson, 1966	*L. kaitiensis* * Ghent and Henderson, 1966	(= *Scolicia*) [1]	" "	" "
		Subphyllochorda Götzinger and Becker, 1932	*S. goa* Vassoievich, 1951	(= *Scolicia*) [1]	" "	" "
			S. granulata Książkiewicz, 1970	" "	" "	" "
			S. laevis Książkiewicz, 1970	" "	" "	" "
			S. striata Książkiewicz, 1970	" "	" "	" "
		Taphrhelminthoida Książkiewicz, 1977	*T. convoluta* * Książkiewicz, 1977	(= *S. strozzii*) [1]	" "	" "
			T. plana (Książkiewicz, 1970)	" "	" "	" "
			T. dailyi Hofmann and Patel, 1989	" "	" "	" "
		Taphrhelminthopsis Sacco, 1888	*T. auricularis* Sacco, 1888	(= *S. strozzii*) [1]	" "	" "
			T. expansa Sacco, 1888	" "	" "	" "
			T. pedemontana (Sacco, 1888)	" "	" "	" "
			T. recta Sacco, 1888	" "	" "	" "
			T. subauricularis Chiplonkar and Badve, 1970	" "	" "	" "
			T. circularis Crimes et al., 1977	" "	" "	" "
			T. yuananensis Li and Yang, 1988	" "	" "	" "
	Bioerosion	*Circolites* Mikuláš, 1992	*C. kotoncensis* * Mikuláš, 1992		J. / t.	DO
		Ericihnus Santos et al., 2015	*E. bromleyi* * Santos et al., 2015		L.M. / t.	AGR PAS
			E. asgaardi Santos et al., 2015		" "	" "
		Gnathichnus Bromley, 1975	*G. pentax* * Bromley, 1975		T. / t.	PAS
			G. stellarum Breton et al., 1992	(= *G. pentax*) [2]	" "	" "
		Roderosignus Michalík, 1977	*R. quinqueradialis* * Michalík, 1977	(= *Gnathichnus pentax*) [2]	" "	" "
		Planavolites Mikuláš, 1992	*P. homolensis* * Mikuláš, 1992		E.K.	PAS DO
HOLOTHURIAN TRACES	Bioturbation	*Artichnus* Zhang et al., 2008	*A. pholeoides* * Zhang et al., 2008		E. / M.	DO
			A. giberti Belaústegui et al., 2014		" "	" "
ASTEROZOAN TRACES	Bioturbation	*Arcichnus* Sutcliffe, 1997	*A. saltatus* * Sutcliffe, 1997		E.D.	REP
			A. lumbricalis * von Schlotheim, 1820	(= *Heliophycus seilacheri*) [3]	Cam. / t.	CUB
			A. pannulatus von Schlotheim, 1820	pseudofossil [4]	" "	" "
			A. ophiurus von Schlotheim, 1820	ophiuroid body fossil [4]	" "	" "
		Asteriacites von Schlotheim, 1820	*A. stelliforme* (Miller and Dyer, 1878)		" "	" "
			A. quinquefolius (Quenstedt, 1876)		" "	" "
			A. gugelhupf Seilacher, 1983	(= *Pentichnus gugelhupf*) [5]	" "	" "
			A. aberensis Crimes and Crossley, 1991	(= *A. quinquefolius*) [4]	" "	" "
			A. obtusus Carrasco, 2011	(= *A. quinquefolius*) [4]	" "	" "
		Heliophycus Miller and Dyer, 1878	*H. stelliforme* * Miller and Dyer, 1878	(= *Asteriacites stelliforme*) [4]	" "	" "
			H. seilacheri Schlirf, 2012	(= *Asteriacites lumbricalis*) [4]	" "	" "
		Biformites Linck, 1949	*B. insolitus* * Linck, 1949	[3]	M.T. / M.	CUB REP
			B. zhadaensis (Yang and Song, 1985)	[4]	" "	" "
		Ophioichnus Bell, 2004	*O. aysenensis* * Bell, 2004	(= *Biformites zhadaensis*) [4]	" "	" "
		Zhadaichnus Yang and Song, 1985	*Z. zhadaensis* * Yang and Song, 1985	(= *Biformites zhadaensis*) [4]	" "	" "
		Pentichnus Maerz et al., 1976	*P. pratti* * Maerz et al., 1976		L.Car.	FOD
			P. gugelhupf (Mángano et al., 1999)		" "	" "
CRINOID TRACES	Bioturbation	*Krinodromos* Neto de Carvalho et al., 2016	*K. bentou* * Neto de Carvalho et al., 2016		M.J.	MOR
MITRATE TRACES	Bioturbation	*Vadichnites* Rahman et al., 2009	*V. transversus* * Rahman et al., 2009		E.D.	MOR

to the presence of subanal tuft spines and corresponding tube feet of the echinoid tracemaker. Among modern spatangoids, the traces produced by the so-called *Spatangus* group exhibit a double drainage, while those generated by the *Echinocardium* group have a single one (Plaziat and Mahmoudi, 1988). Various aquaria experiments have also shown that spatangoids may be fast and effective burrowers. For example, the large tropical species *Moira atropos* burrows at speeds of 2 cm/h and moves about 5 cm^3 of sediment per hour (see Gingras et al., 2008).

The ichnotaxa *Subphyllochorda* Götzinger and Becker, 1932, *Taphrhelminthopsis* Sacco, 1888 and *Taphrhelminthoida* Książkiewicz, 1977 were included in *Scolicia* by Uchman (1995). This author regarded *Subphyllochorda* as the sole expression of *Scolicia*, *Taphrhelminthopsis* as a cast of washed-out *Subphyllochorda* or *Scolicia*, and *Taphrhelminthoida* as having the same morphology as that of *Taphrhelminthopsis*. Uchman (1995) also considered the ichnogenus *Laminites* Ghent and Henderson, 1966 as a preservational expression of different types of traces (*Scolicia*, *Bichordites* and other non-echinoid Palaeozoic burrows), lacking diagnostic features and only useful in order to informally characterize a particular preservational variant (Fig. 1.13).

Smith and Crimes (1983) erected the ichnogenus *Cardioichnus* to designate ovate to sub-quadrate, bilobed resting traces (cubichnia) (Figs. 1.15, 2.5–2.7), which are commonly associated with *Scolicia* or *Bichordites* (e.g., Mayoral and Muñiz, 2001; Bernardi et al., 2010); its fossil record ranges from the Late Cretaceous to the early Pliocene.

It is known that, among modern echinoids, clypeasteroids are able to produce several bioturbation structures (e.g., Seilacher, 1979). Since the majority of these traces are surficial and are found in higher energy environments, they have a very low preservation potential and have not yet been identified in the fossil record (Figs. 1.6, 2.8). For example, Bell and Frey (1969) described the burrowing activity of the clypeasteroid *Mellita quinquiesperforata* and figured the surficial trails or the aggregations of small pits (linked with their five lunules) left by these sand dollars.

Echinoid bioerosion structures.—The ichnogenera *Gnathichnus* Bromley, 1975, *Circolites* Mikuláš, 1992, *Planavolites* Mikuláš, 1992 and *Ericichnus* Santos et al., 2015 are unique bioerosion structures attributed to echinoderms, in particular to regular echinoids (e.g., Bromley, 1975; Warme, 1975; Martinell, 1981, 1982, 1989; Meyer, 2011; Gibert et al., 2012; Schönberg and Wisshak, 2014). Echinoid bioerosion may also have been very important in modern environments (e.g., Bronstein and Loya, 2014 and references therein).

Gnathichnus corresponds to bite traces produced by echinoids plucking and grazing by using their jaw apparatus (and occasionally also their spines) on both organic and inorganic hard substrates (Figs. 1.1, 3.2). They are known from the Triassic and are very common in modern environments (see Bromley,
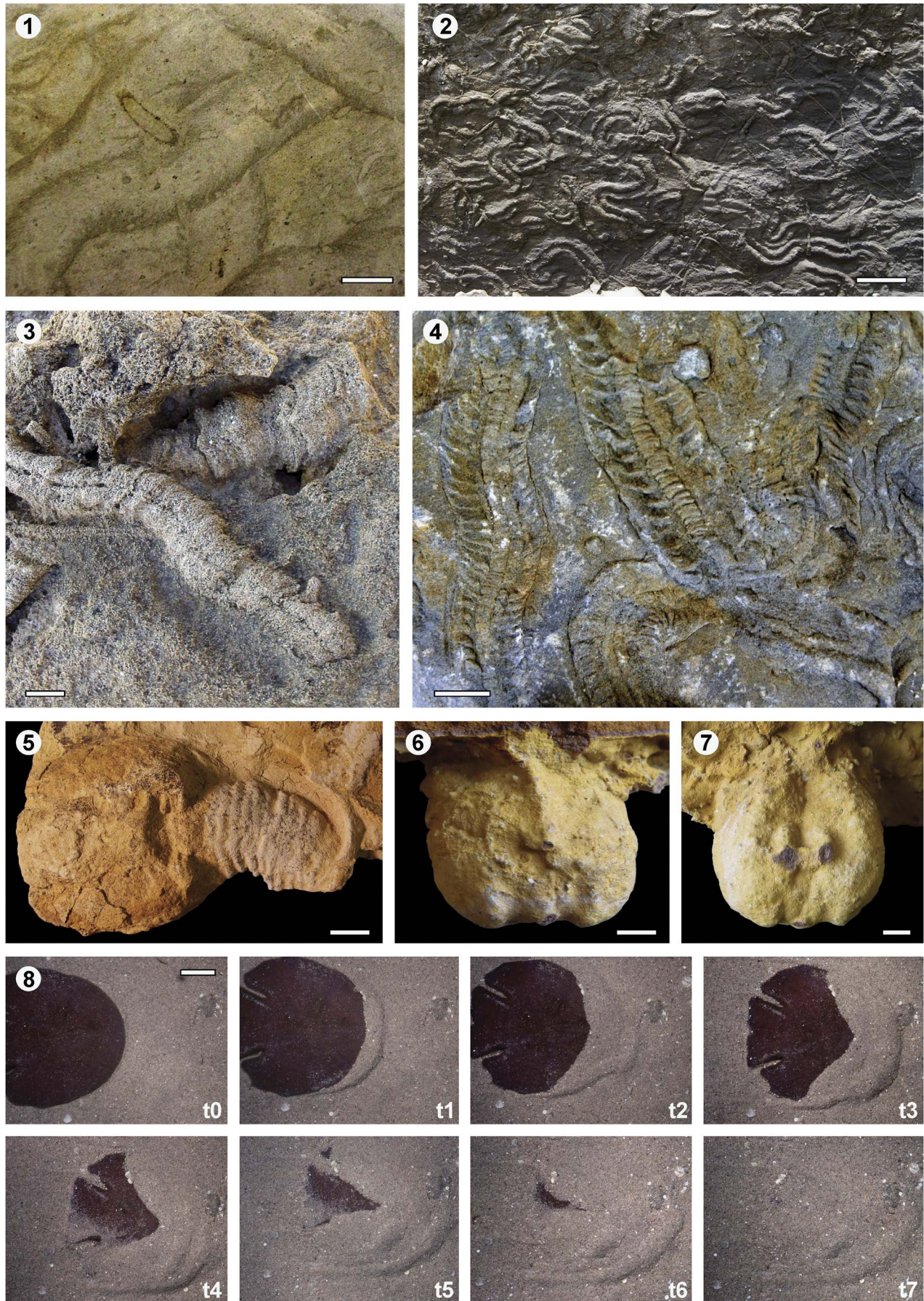
2004 and references therein). In addition, the *Gnathichnus* ichnofacies proposed by Bromley and Asgaard (1993) highlighted the importance of this ichnotaxon as a component of trace fossil assemblages that record short-term bioerosion (praedichnia, pascichnia and fixichnia) in shellgrounds associated with moderate energy settings since the Jurassic (Gibert et al., 2007; Buatois and Mángano, 2011). In addition, Radwańska (1999) regarded the ichnogenus *Roderosignus* Michalík, 1977 and the ichnospecies *Gnatichnus stellarum* Breton, Neraudeau and Cuenca-Boulat, 1992 as synonyms of *Gnathichnus* and *G. pentax* Bromley, 1975, respectively.

Circolites consists of bowl-shaped, hemispherical or deeper pits bored in hard or firm substrates and related to shallow waters (Figs. 1.3, 3.1, 3.4); its range is from the Jurassic to the Recent (e.g., Kempf, 1962; Peres and Picard, 1964; Gibert et al., 1998; Bromley, 2004 and references therein). These bioerosion structures are mechanically produced in different kinds of substrates consisting of both sedimentary and non-sedimentary rocks (see table 1 of Santos et al., 2015). These traces have been recorded from a wide variety of substrates including beach rocks (Fig. 3.3), carbonate (e.g., Martinell and Domènech, 1986; Domènech et al., 2014), granite (e.g., Martinell, 1981), or basalt (e.g., Ramalho et al., 2010); for example, in the case of granite, despite the fact that some of the components (e.g., quartz and feldspar) have a higher hardness than their teeth, echinoids are able to perforate these rocks using their jaw apparatus and spines to firstly detach the softer micaceous grains, which subsequently allows an easier and faster detachment of harder grains (Martinell, 1981). Schoppe and Werding (1996), describing the *Circolites*-like borings generated by the modern echinoid *Echinometra lucunter* in the Caribbean coast of Colombia, highlighted the presence of several organisms (as crabs, clingfish or brittle stars) cohabiting within these boreholes.

Ericichnus comprises a system of grooves with a sinuous pathway, which may be associated with isolated *Circolites* (Figs. 1.2, 3.5; Santos et al., 2015). Two ichnospecies have been described (Table 1; Santos et al., 2015): *E. bromleyi* from late Miocene to early Pliocene rocks of Santa Maria Island (Azores, Portugal), and *E. asgaardi* from the early Miocene of Foz da Fonte (Portugal). This kind of structure is also very common in modern settings (Fig. 3.3, 3.5).

Finally, *Planavolites* was erected by Mikuláš (1992) in the early Cretaceous of the Czech Republic. This ichnogenus consists of flat and large depressions with an irregular oval or very elongated form, and was attributed to the continued boring activity of several generations of chitons, gastropods and echinoids (Mikuláš, 1992). Following Santos et al. (2015), *Planavolites* and *Ericihnus* may be considered separate ichnogenera by: (1) displaying a different general structure and dimensions (while *Planavolites* is a simple and single structure, *Ericichnus* constitutes a complex system); and (2) the presence

$\longrightarrow$

Figure 2. Echinoid bioturbation: **(1)** *Bichordites* ichnofabric (horizontal section) from the Miocene Bateig Limestone (Alicante, SE Spain; see Gibert and Goldring, 2008); **(2)** *Scolicia* isp. from the Eocene of Zumaia (Gipuzkoa, N Spain); **(3)** *Bichordites monastiriensis* from the early Pliocene of the Guadalquivir Basin (Cádiz, SW Spain; see Aguirre et al., 2010); **(4)** *Bichordites* isp. from the Eocene of Zumaia (Gipuzkoa, N Spain); **(5)** *Cardioichnus planus* associated to *Scolicia* isp. from the Pliocene of Sant Feliu de Llobregat (Barcelona, NE Spain); **(6, 7)** *Cardioichnus reniformis* from the Miocene of the Guadalquivir Basin (Lepe, Huelva, SW Spain), upper and lower views respectively; and **(8)** digging process of the sand dollar *Echinodiscus auritus* in the Red Sea (t0 to t7 time lapse is 1 minute). Scale bars are **(1, 2)** 5 cm; **(3, 8)** 2 cm; **(4, 5, 6, 7)** 1 cm.
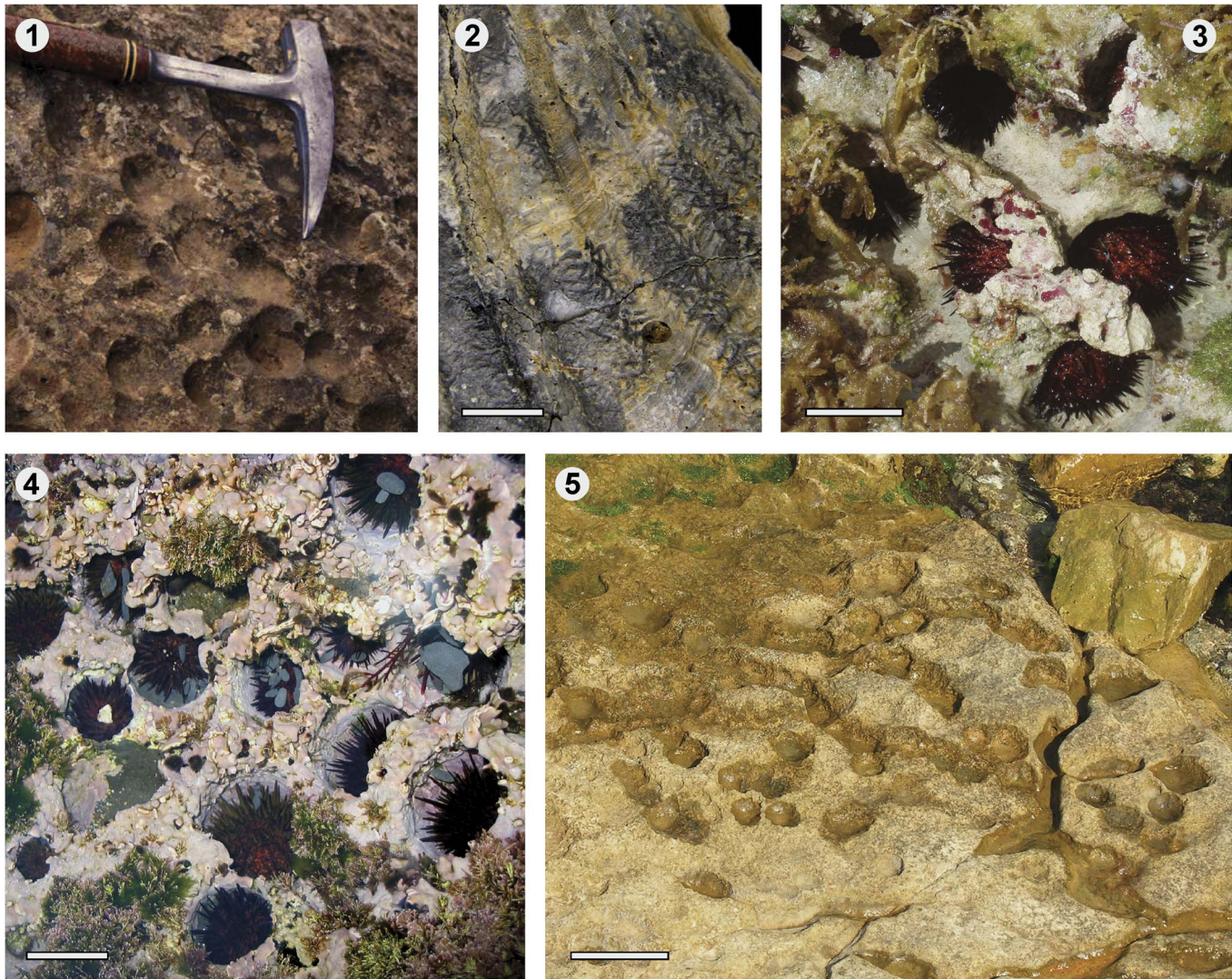
Figure 3. Echinoid bioerosion: **(1)** *Circolites* isp. from the Pliocene of Viladamat (Girona, NE Spain); **(2)** *Gnathichnus pentax* on the outer side of a pectinid valve from the Pliocene Roussillon Basin (SE France); **(3)** borings (*Ericichnus*-like) produced by regular echinoids (*Echinometra lucunter*) in a beach rock from San Salvador Island (Bahamas); **(4)** Specimens of *Paracentrotus lividus* boring hemispherical pits in the rocky coast of l'Estartit (Girona, NE Spain); and **(5)** modern *Ericichnus*-like borings, probably produced by *Paracentrotus lividus*, in the coast of Salou (Tarragona, NE Spain). Scale bars are **(2)** 0.5 cm; **(3, 4)** 5 cm; **(5)** 10 cm.

of *Circolites* associated along the *Ericihnus* systems (this is absent in *Planavolites*).

Holothurian bioturbation structures.—Sea cucumbers are very important epi- and infaunal burrowers in modern seas (e.g., Dashtgard and Gingras, 2012; Ayranci and Dashtgard, 2013). At the moment, however, only the ichnogenus *Artichnus* Zhang et al., 2008 has been attributed to the burrowing activity of holothurians. *Artichnus* consists of J- or 'test tube'-shaped, cylindrical and blind burrows with a thick laminated lining which may consist of retrusive spreiten (Zhang et al., 2008; Belaústegui et al., 2014). At the moment, only two ichnospecies have been described: *A. pholeoides* Zhang et al., 2008 in the Eocene of Poland and *A. giberti* Belaústegui, Domènech and Martinell, 2014 in the Miocene of northeastern Spain (Figs. 1.5, 4.1, 4.2). Additionally, in the middle Miocene of the Algarve region (southern Portugal), Santos et al. (2014) described a series of dwelling/equilibrium bioturbation structures that are

attributed to the burrowing activity of gastrochaenid bivalves. Their descriptions and figures, however, fit perfectly with that of the ichnospecies *A. giberti* and the ichnogeneric assignment of this material should be revised.

Modern infaunal sea cucumbers are classified in three orders: Dendrochirotida, Molpadiida and Apodida (Nichols, 1969; Ayranci and Dashtgard, 2013). Some of them may construct simple burrows projecting the tentacles or the anus to the surface (e.g., Ruppert et al., 2004), or U-shaped burrows projecting both outside the sediment (e.g., Frey and Howard, 1972; Bromley, 1990; Smilek and Hembre, 2012) (Fig. 1.4, 1.5). This is because some holothurians must have the anus in contact with seawater for respiratory functions (Fretter and Graham, 1976; Ruppert et al., 2004; Zhang et al., 2008). Fretter and Graham (1976) pointed out that the most efficient holothurian burrowers are the vermiform, apodous forms belonging to the family Synaptidae (order Apodida), which burrow by means of the tentacles and the muscular action of the
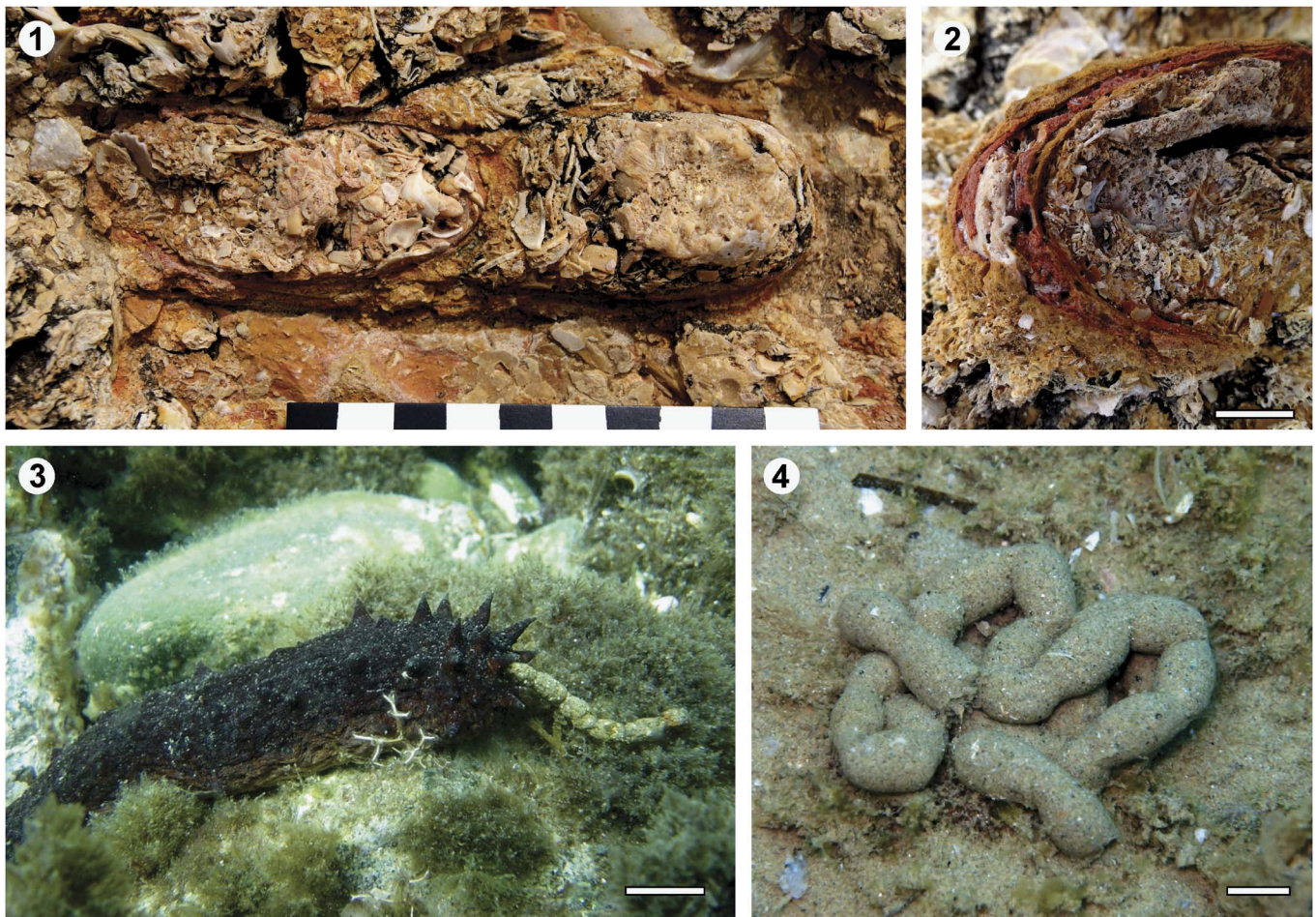
Figure 4. Holothurian bioturbation: **(1, 2)** *Artichnus giberti* from the Miocene of El Camp de Tarragona Basin (NE Spain; see Belaústegui et al., 2014); and **(3, 4)** *Holothuria tubulosa* from the Cap de Creus (Girona, NE Spain), and detail of its excrements (Photographs courtesy of M. Ballesteros). Scale bars are **(2, 4)** 1 cm; **(3)** 3 cm.

body; they do not need to project the anus above the substratum for respiration (Fretter and Graham, 1976).

More recent neoichnological studies have shown how different holothurian taxa are able to excavate burrows comparable to the ichnogenera *Arenicolites*, *Artichnus*, *Asterosoma*, *Diplocraterion*, *Skolithos* or *Thalassinoides*, as well as surficial mounds and funnel-shaped structures (Dashtgard and Gingras, 2012; Ayranci and Dashtgard, 2013). Finally, it is known that deposit-feeding sea cucumbers produce a great amount of excrement during life. These excretions consist of more or less continuous cylinders of processed sediment, which commonly exhibit equidistant constrictions along their length (Fig. 4.3, 4.4). They have, however, not yet been described in the fossil record.

Asterozoan bioturbation structures.—In the fossil record, the most common traces attributed to asterozoans have been interpreted as resting traces (cubichnia) and included within the ichnogenus *Asteriacites* von Schlotheim, 1820. *Asteriacites* consists of star-shaped impressions, commonly with five radial arms that taper distally (Figs. 1.7, 5.1, 5.2) (Seilacher, 1953; Knaust and Neumann, 2016). Due to the lack of type material, Schirlf (2012) considered *Asteriacites* as a nomen dubium and proposed its synonymy with *Heliophycus* Miller and Dyer,

1878. Knaust and Neumann (2016) have, however, recently rediscovered von Schlotheim's type material, confirming the legitimacy of *Asteriacites* as a valid ichnogenus, and consequently keeping *H. stelliforme* (the type ichnospecies) as synonym of *A. stelliforme*, as already proposed Osgood (1970). This ichnogenus is very common from the Cambrian to the Recent (Table 1; e.g., Hess, 1983; Crimes and Zhiwen, 1986; Mikuláš, 1990; Mángano et al., 1999; Jagt et al., 2009; Gurav et al., 2014; Baucon and Neto de Carvalho, 2016); since the older record of *Asteriacites* predate the first asteroid body fossil evidence (Ordovician; see Clarkson, 1998), this could suggest that these organisms had already evolved from the Cambrian. Neoichnological observations have allowed noting that while starfish resting traces are morphologically more consistent, those produced by brittle stars may exhibit more variations due to the greater mobility of their arms (Seilacher, 1953, 2007; Ishida et al., 2004, 2013).

Four ichnogenera have been interpreted as the locomotion traces produced by asteroids and/or ophiuroids: *Biformites* Linck, 1949, *Zhadaichnus* Yang and Song, 1985 (see also Yang et al., 2004), *Arcichnus* Sutcliffe, 1997 and *Ophioichnus* Bell, 2004. Although initially Knaust et al. (2014) proposed *Ophioichnus aysensis* Bell, 2004 as a junior subjective synonym of *Zhadaichnus zhadaensis* Yang and Song, 1985, Knaust and
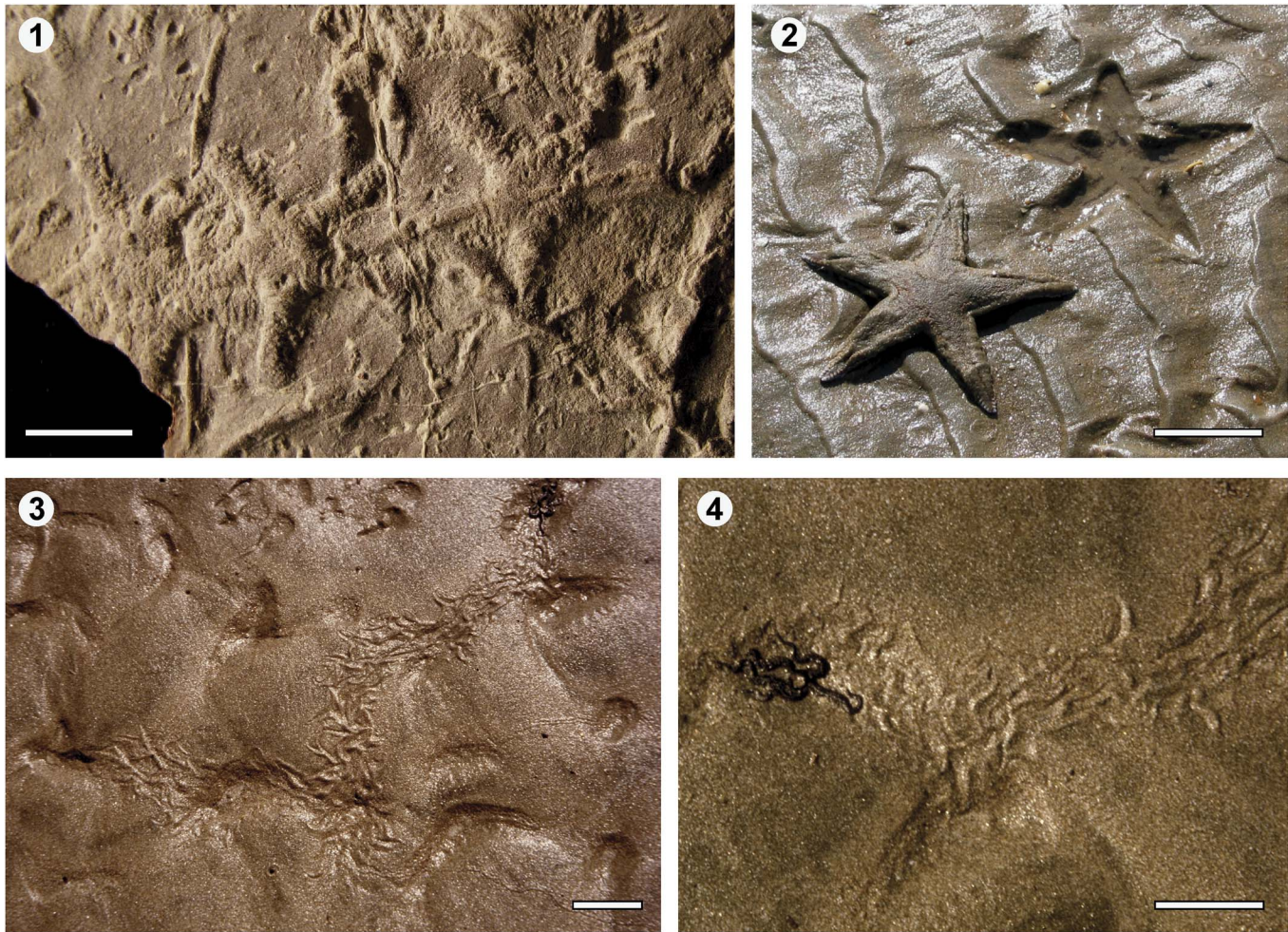
Figure 5.   Asterozoan bioturbation: **(1)** *Asteriacites* isp. from the Eocene of Tavertet (Barcelona, NE Spain); **(2)** *Astropecten irregularis* and its resting trace (*Asteriacites*-like) in the Nueva Umbría Spit (Lepe, Huelva, SW Spain); and **(3, 4)** ophiuroid locomotion traces from Punta Chivato (Baja California, Mexico). Scale bars are **(1)** 0.5 cm; **(2)** 10 cm; **(3, 4)** 5 cm.

Neumann (2016) ultimately considered *Ophioichnus* and *Zhadaichnus* as synonyms of *Biformites*. In any case, these three ichnotaxa consist of isolated or clustered hook-shaped impressions (see Knaust and Neumann, 2016) and are recorded from the Middle Triassic to the Miocene (Figs. 1.8, 1.9, 5.3, 5.4; Table 1). Locomotion traces of modern ophiuroids, very similar to *Biformites*/*Ophioichnus*/*Zhadaichnus*, were also figured by Schäfer (1972). By contrast, *Arcichnus* is characterized by an alternation (i.e., trackway) of horseshoe-shaped and straight tracks, which has been described in the Early Devonian of Germany (Sutcliffe, 1997).

Finally, the ichnogenus *Pentichnus* Maerz, Kaesler and Hakes, 1976, consisting of conical burrows with pentameral symmetry, was interpreted as the result of ophiuroid or asteroid burrowing activity; stalked crinoids were also proposed as possible tracemakers (Rindsberg, 1994). Although Chamberlain (1971) and Seilacher (1983) interpreted these burrows as resting traces and included them within *Asteriacites* (as *A. lumbricalis* 'hiding form' and *A. gugelhupf*, respectively), subsequent authors agreed to separate these traces as different structures, i.e., domichnia instead of cubichnia (Mikuláš, 1990; Rindsberg, 1994; Mángano et al., 1999). In fact, Mángano et al. (1999) proposed to better regard *A. gugelhupf* as *Pentichnus gugelhupf*.

Pentichnus has been mainly recorded from Carboniferous sedimentary rocks (see Table 1).

Although they have not yet been identified in the fossil record, additional burrowing behaviors as well as bioturbation structures conducted and produced by modern brittle stars are known. Morton and Miller (1968) described and figured the manner in which the species *Amphiura aster* lives permanently buried (only the distal parts of their arms in contact with the surface) in spring-tidal flats of the New Zealand sea shore. Christensen and Colacino (2000), through aquarium observations, also described and figured the burrowing behavior of the brittle star *Hemipholis elongata*, which is very similar to those of *A. aster* (Fig. 1.10).

Asterozoan bioerosion structures.—Asterozoans, mainly asteroids, are very active predators (e.g., Carter, 1968), and there are even records of fossil sea stars showing the typical feeding posture (i.e., a humped posture over their prey with the arms wrapping around; see Blake and Guensburg, 1994). The record of modern or fossil bioerosion structures preserved in the skeleton of their prey is, however, very rare. Gordillo and Archuby (2012), under aquarium conditions, described how the periostracum (conchiolin layer) of the area around the byssus of

mussel shells was removed by the action of acids discharged by the asteroid *Cosmasterias lurida* during predation. It seems, however, very unlikely that these traces can be recognized in the fossil record. It was also reported by Gordillo and Archuby (2012) that, although some of the mussel shells may be crushed during these attacks, the resulting fracture patterns are indistinguishable from those caused by physical factors.

Crinoid bioturbation structures.—Most crinoids exhibit a sessile lifestyle, but it is known that some stalked crinoids (comatulids and isocrinids) are able show locomotion. Although some aquarium observations have been carried out (e.g., Messing et al., 1988), Baumiller and Messing (2007) recorded for the first time the active locomotion of the isocrinid *Neocrinus decorus* by in situ observation with a submersible at a depth of 420 m near Grand Bahama Island. The resulting traces produced by the 'elbow-crawl' locomotion (Baumiller and Messing, 2007) consist of a central and rectilinear groove (i.e., the mark left by the drag of the stalk) probably flanked by the imprints of the power strokes of the arms (Fig. 1.11). Since the submarine video filmed by Baumiller and Messing (2007) only permits clear observation of this central groove, these authors also figured the traces produced by the crawling comatulid *Davidaster rubiginosa* on a muddy substrate under aquarium condition; proposing that these traces could be comparable with those left by the arms of the isocrinid *N. decorus*.

Recently and for the first time in the trace fossil record, Neto de Carvalho et al. (2016) observed a definite crinoid crawling trace and erected the new ichnotaxon *Krinodromos bentou*. This trace fossil consists of an irregular trail, bordered by shallow and large grooves, associated at its very end with an isocrinid crinoid body fossil from the Middle Jurassic of the Cabeço da Ladeira Lagerstätte (Portugal).

Despite the good knowledge of the different anchoring strategies of crinoids in soft sediments (Seilacher and MacClintock, 2005; Donovan, 2006), some of which are potential producers of bioturbation structures, no modern or fossil traces have been ascribed to them.

Traces associated with mitrate body fossils.—Associated with body fossils of the Devonian stylophoran *Rhenocystis latipedunculata*, Rahman et al. (2009) erected the ichnotaxon *Vadichnites transversus* as horizontal straight to curved traces with low relief protuberances or closely spaced fine ridges transversely oriented across a shallow groove. This new ichnotaxon is argued to demonstrate that the appendage of *R. latipedunculata* was used in locomotion and that this movement took place appendage-first. Rahman et al. (2009) interpreted these trace fossils as having been produced just before death probably in response to catastrophic burial by turbidity current deposits. Although Vallon et al. (2016) do not recommended the use of this ethological category, arguing that it is based on holistic interpretations, rather than on trace fossil morphology, the ichnogenus *Vadichnites* could be considered as an example of mortichnia.

Finally, in order to obtain a rapid understanding of all these ichnotaxa, a recompilation of ichnogenera diagnoses is shown in Table 2. According to the last ichnotaxonomic studies, only the diagnoses of those broadly accepted ichnogenera have been included.

Traces not directly produced by echinoderms but closely related to them

Echinoderms possess multi-element skeletons composed of thousands of diverse ossicles (e.g., Donovan, 1991; Kroh and Nebelsick, 2010). After death and under 'normal' conditions (i.e., excluding rapid burials, dysoxic conditions, etc.), the disarticulation of most parts of echinoderm skeletons, except for many echinoids that are commonly preserved as complete denuded tests (see Belaústegui et al., 2012 and references therein), is very fast (days to weeks) and their separate single ossicles may become very important components within the sediment (Ausich, 1997; Kroh and Nebelsick, 2010; Dynowski, 2012). Occasionally, the abundance of these ossicles on the seafloor may be condensed by the activity of burrowing organisms (e.g., the ichnogenus *Crininicaminus*, see below). In addition, the unique compositional and morphological features of the echinoderm skeletons promote their rapid growth and regeneration (Kroh and Nebelsick, 2010). These qualities may facilitate the preservation of an ichnological record (e.g., predation, parasitism) on or in their skeletons.

Traces produced with or in echinoderm ossicles and/or spines.—Ettensohn (1981) erected the ichnogenus and ichnospecies *Crininicaminus haneyensis*, to describe cylindrical burrows with a lining mainly composed of crinoids ossicles from the Carboniferous of east-central Kentucky, USA. Subsequently, from the late Permian Kamiyasse Formation (northeastern Japan), Seike et al. (2014) erected the new ichnospecies *C. giberti* differing from *C. haneyensis* by the arrangement of the crinoid stem plates (horizontal to the long axis of the tunnel in *C. haneyensis*, and vertical in *C. giberti*). In both cases, the authors attributed its probable construction to the burrowing activity of tube-dwelling worms.

Neumann et al. (2008) erected the ichnospecies *Trypanites mobilis* for borings produced in bulbous spines of psychocidarid echinoids from the Late Cretaceous (Cenomanian) to early Paleocene (Danian) strata of the North Sea Basin (Denmark). These authors proposed that these borings were produced post-mortem by sipunculid worms, which would have used these spines as mobile domiciles on soft-bottom habitats.

Bioclaustrations on echinoderm stereom.—Embedment structures or bioclaustrations consists of cavities produced by endosymbiontic organisms that live within, by partially inhibiting, the growing skeleton of a host organism (e.g., Tapanila, 2005; Cónsole-Gonella and Marquillas, 2014). Tapanila (2005) included all these traces within the new ethological category Impedichnia; although subsequent authors do not recommend its use (Vallon et al., 2016, and references therein). In any case, bioclaustrations produced in the stereom of different echinoderms, mainly crinoids, have been recorded and several ichnotaxa have been erected to name them.

The ichnogenus *Tremichnus* was erected by Brett (1985) to include simple circular-parabolic pits, with or without associated stereom swellings, primarily produced by a combination of embedment (i.e., inhibition of stereom growth) and true

Table 2. Ichnogenera diagnoses. According to the last ichnotaxonomic discussions, only diagnoses of those broadly accepted ichnogenera have been included.

		ICHNOTAXA	Ichnogenus DIAGNOSES
ECHINOID TRACES	Bioturbation	*Bichordites* Plaziat and Mahmoudi, 1988	"Predominantly horizontal, cylindrical or subcylindrical, straight to winding, unbranched, meniscate, complex burrow with a central bilobate core." (emended by Demírcan and Uchman, 2012)
		Cardioichnus Smith and Crimes, 1983	"Resting trace preserved as positive features sandstone soles. Ovate to sub-quadrate in outline consisting of two curved lateral lobes which merge anteriorly and may be faintly marked with fine, impersistent lineations, and a central depressed, V-shaped area sometimes surrounded by a weak rim. The central region is covered in strong prod marks. May be continuous with the repichnia *Scolicia* or isolate." (after Mayoral and Muñiz, 2001)
		Scolicia de Quatrefagues, 1849	"Variable and commonly selectively preserved, simple, winding, meandering to coiling bilobate or trilobate back-filled trace fossil with two parallel, locally discontinuous, sediment strings along their underside. Cross-section approximately oval in outline. Underside between the strings flat or slightly convex up. Backfill laminae composite, may be biserial on the upper side. Washed-out variants preserved as hypichnial bilobate ridges." (emended by Uchman, 1998)
	Bioerosion	*Circolites* Mikuláš, 1992	"Shallow, roughly circular pits in carbonate substrates. The peripheral edge of the pit is sharp, the walls of the pit are perpendicular to or overhanging the substrate surface. The edges of some pits are undulated, the pit bottom is moderately concave." (after Mikuláš, 1992)
		Ericichnus Santos et al., 2015	"Grooves relatively deep, with sinuous pathway, with a width fairly uniform along its trajectory. Often they show points where the path is bifurcated reaching, in these cases, a width which can be the double of the normal diameter. Inside there are a number of lines or marks, more or less pronounced, with a concavity oriented in the animal's direction of movement." (Santos et al., 2015)
		Gnathichnus Bromley, 1975	"Biogenic sculpture consisting of grooves, pits, and scratches on hard substrate." (Bromley, 1975)
		Planavolites Mikuláš, 1992	"Flat, considerably large depressions of irregular oval or very elongated form, occurring on the surface of a firm limestone substrate, The outline is undulated, sometimes lobate, even with pointed prejections. The bottom is rounded, more or less smooth, in some individuals with flat protrusions or depressions. The walls are usually steep, perpendicular or slightly overhanging; borings often occur in large groups." (after Mikuláš, 1992)
HOLOTHURIAN TRACES	Bioturbation	*Artichnus* Zhang et al., 2008	"Wide J-shaped, generally cylindrical structure, turbinate in the distal part towards the blind termination, and tapering in the proximal part. The proximal part comprises a steeply upward bent, narrowing shaft, tapering upwards. The burrow lumen lies within a thickly laminated, short, vertical, mostly retrusive spreite, which is best developed in the lower part of the structure. The outer margin is longitudinally striated in some specimens." (Zhang et al., 2008)
ASTEROZOAN TRACES	Bioturbation	*Arcichnus* Sutcliffe, 1997	"Horizontally oriented horseshoe- to U-shaped tracks opening in a constant direction." (Sutcliffe, 1997)
		Asteriacites von Schlotheim, 1820	"Star-shaped, commonly pentamerous impressions with arms grading from a central area and continuously tapering distally." (Knaust and Neumann, 2016 after Seilacher, 1953)
		Biformites Linck, 1949	"Narrow, bedding-parallel vermiform, hook-shaped and sinuous imprints with slightly tapering terminations, unbranched or with secondary successive branching, with or without ornament." (emended by Knaust and Neumann, 2016)
		Pentichnus Maerz et al., 1976	"Subcylindrical to subconical burrows with poorly to well-developed pentameral symetry." (emended by Knaust and Neumann, 2016)
CRINOID TRACES	Bioturbation	*Krinodromos* Neto de Carvalho et al., 2016	"Trails composed of a narrow and flat central area with an irregular winding furrow, or almost no sedimentary disruption, bordered by shallow and large grooves externally limited by irregular piles of sediment." (Neto de Carvalho et al., 2016)
MITRATE TRACES	Bioturbation	*Vadichnites* Rahman et al., 2009	"Horizontal straight to curved traces characterized by low relief protuberances or closely spaced fine ridges transversely oriented across a shallow groove." (Rahman et al., 2009)

boring (i.e., removal of stereom), on echinoderms (mainly crinoids; Fig. 6.8) (see also, Brett, 1978; Eckert, 1988; Feldman and Brett, 1998; Wilson et al., 2014; Donovan, 2015; Vinn et al., 2015). Brett (1985) proposed parasites or commensal filter feeders as possible tracemakers. The stratigraphic record of *Tremichnus* ranges from the Middle Ordovician to the Middle Jurassic. In addition, an important ichnotaxonomic discussion has been developed around this ichnogenus together with *Oichnus* Bromley, 1981, *Sedilichnus* Müller, 1977 and *Fossichnus* Nielsen, Nielsen and Bromley, 2003. Pickerill and

Donovan (1998) regarded *Tremichnus* as junior synonym of *Oichnus*. Bromley (2004) followed this synonymy and in turn considered *Sedilichnus* as their possible senior synonym; nevertheless Bromley (2004) kept using *Oichnus*. Subsequently, Zonneveld and Gingras (2014) formalized all these proposals and established *Tremichnus*, *Oichnus* and *Fossichnus* as junior synonyms of *Sedilichnus*. Finally, Wisshak et al. (2015) noted that *Sedilichnus* is an atelonym and has no nomenclatural value. Consequently, they retained *Oichnus* and *Tremichnus* as valid ichnogenera and pointed out their

respective synonyms *Fossichnus* and *Balticapunctum* Rozhnov, 1989. Wisshak et al. (2015; see emended and differential diagnoses) differentiated *Oichnus* from *Tremichnus* because this latter is restricted to echinoderm host substrates and does not penetrate through the substrate.

Two names, *Myzostomites* and *Schizoproboscina*, were firstly and respectively proposed by Clarke (1921) and Yakolev (1939) to designate swelling- or cyst-like structures produced by parasites on echinoderms, mainly crinoids and echinoids. Radwańska and Radwański (2005), studying the myzostomid and copepod infestation of Jurassic echinoderms, revised the taxonomic validity of these names and highlighted that: (1) *Myzostomites* has been treated both as a body fossil (the worm *M. clarkei* Howell, 1962) and a trace fossil (Häntzschel, 1975), (2) *Schizoproboscina* (with its species *S. ivanovi* Yakolev, 1939) was accepted as a worm body fossil by Howell (1962), and (3) the *Schizoproboscina* material described by Yakolev (1939) and revised by Arendt (1961) shares many similarities with the *Myzostomites* type material of Clarke (1921). Radwańska and Radwański (2005) regarded *Schizoproboscina* as a junior synonym of *Myzostomites*, and consequently, *M. ivanovi* (Yakovlev, 1939) as the valid name for the type material of Clarke (1921). Additionally, Brett (1985) proposed to replace *M. clarkei* with *Tremichnus cysticus* Brett, 1985; however, Radwańska and Radwański (2005) considered this modification invalid according to the ICZN rules. Following Radwańska and Radwański (2005), the ichnogenus *Myzostomites* (Yakolev, 1939) should comprise paired round borings connected by an internal U-shaped canal produced on echinoderms (mainly crinoids), which in most cases promotes an overgrowth (swelling-like or cyst) of their stereom.

Castexia Mercier, 1936 includes spherical endocysts, convexly elevated upon the echinoid test, with a pentagonal or subdecagonal outline, and five to 16 teardrop-shaped, periph- erally dispersed orifices (occasionally, a subcentral orifice may occur). The wall of these endocysts is constructed by the stereom overgrowth of the host echinoderm (exclusively echinoids) that reacts to the activity of the producer, thus embedding it. Copepods (Crustacea) have been proposed as probable tracemaker from the Ordovician onward (see extensive review in Klompmaker and Boxshall, 2015). These endocysts are especially prevalent in the Middle to Late Jurassic (Mercier, 1939; Radwańska and Radwański, 2005 and references therein). In addition, Radwańska and Radwański (2005) regarded the ichnotaxon *Canceripustula nocens* Solovyev, 1961 as a junior synonim of *Castexia douvillei* Mercier, 1939.

Radwańska and Radwański (2005) also described 'Halloween pumpkin-mask' cysts consisting of bulbous exo- cysts with numerous circular orifices, recorded on Late Jurassic echinoid tests and more rarely on Early Jurassic crinoid stems. As in the case of *Castexia*, these exocysts have been interpreted as the result of stereom overgrowth promote by copepod parasitism. Similar fossil exocysts or swelling structures have described by Franzen (1974), Smith (1988), Mehl et al. (1991), Radwańska and Poirot (2010) and Klompmaker and Boxshall (2015). It is also known that the modern copepod *Pionodesmotes* Bonnier, 1898 inhabits the internal test surface of live echinoids within galls, which are connected to the exterior by an irregular opening bored through the stereom

(Richard, 1907; Jangoux, 1987). They have, however, not yet been recognized in the fossil record.

Finally, the ichnogenus *Ostiocavichnus* was erected by Bohatý et al. (2012) from Devonian crinoids of Germany and Poland. It comprises gall-like swellings produced on crinoid pluricolumnals by epizoozoan rugose corals. These traces consist of elliptical or subcircular concavities resulting from the encasing of the coral by stereomic coating (Bohatý et al., 2012).

Swelling structures comparable to the ichnogenera cited in this subsection but not ascribed to any of them, and produced by diverse parasites (e.g., myzostomid worms, copepods) on different kinds of echinoderms (mainly crinoids and echinoids, Fig. 6.1, and their spines), have also been described (e.g., Franzen, 1974; Welch, 1976; Werle et al., 1984; Abdelhamid, 1999; Radwańska and Radwański, 2005; Hess, 2010; Thomka et al., 2014; Wilson et al., 2014 and references therein).

Traces produced by symbiosis (mainly parasitism) on echinoderms.—The existence of diverse symbiotic relations between echinoderms and various kinds of organisms have been recorded both in the fossil record and in the Recent (e.g., Tapanila, 2008; Boucot and Poinar, 2010); subsequently, some of these relations may generate an ichnological record.

The parasitism of platyceratid gastropods on crinoids (Fig. 6.9), more rarely on blastoids, is well known and documented in the fossil record (e.g., Baumiller, 1990, 2002, 2003; Baumiller and Gahn, 2002, 2003; Gahn and Baumiller, 2003; Baumiller et al., 2004; Donovan, 2015). Baumiller (1990) described the presence of drill-holes (*Oichnus*-like) on Mississippian crinoids, which are interpreted as the non- predatory drilling activity of platyceratid gastropods. This interpretation is based on the occurrence of a platyceratid shell located just above a conical hole present on the tegmen of one of these Mississippian crinoids. Similar drill holes, also attributed to parasitic platyceratids, have also been documented on Devonian blastoids and crinoids (Baumiller, 1996 and Gahn et al., 2003, respectively).

Circular to subcircular traces, produced on the surface of an early Maastrichtian holasteroid echinoid test (northern Germany), and consisting of a more or less pronounced rim surrounding a central depression, were interpreted by Neumann and Wisshak (2006) as the attachment scars produced by probable parasitic foraminifera during a syn-vivo infestation; since the characteristic rim of these traces would be the result of the host-skeletal overgrowth around the attached parasite as defense mechanism.

Wisshak and Neumann (2006) described 27 U-shaped borings (*Caulostrepsis* isp.) produced on the test of a Late Cretaceous holasteroid echinoid of Germany. Since stereom regeneration is observed in the walls of these borings, these authors interpreted the trace as the result of a symbiotic association (syn-vivo infestation) between boring polychaetes (probably spionids) and the echinoid.

Donovan et al. (2010) interpreted a non-penetrative shallow scar (rounded to pentagonal in outline) present on the test of a Late Cretaceous holasteroid echinoid from the Maastrichtian type area (the Netherlands, Belgium), as the
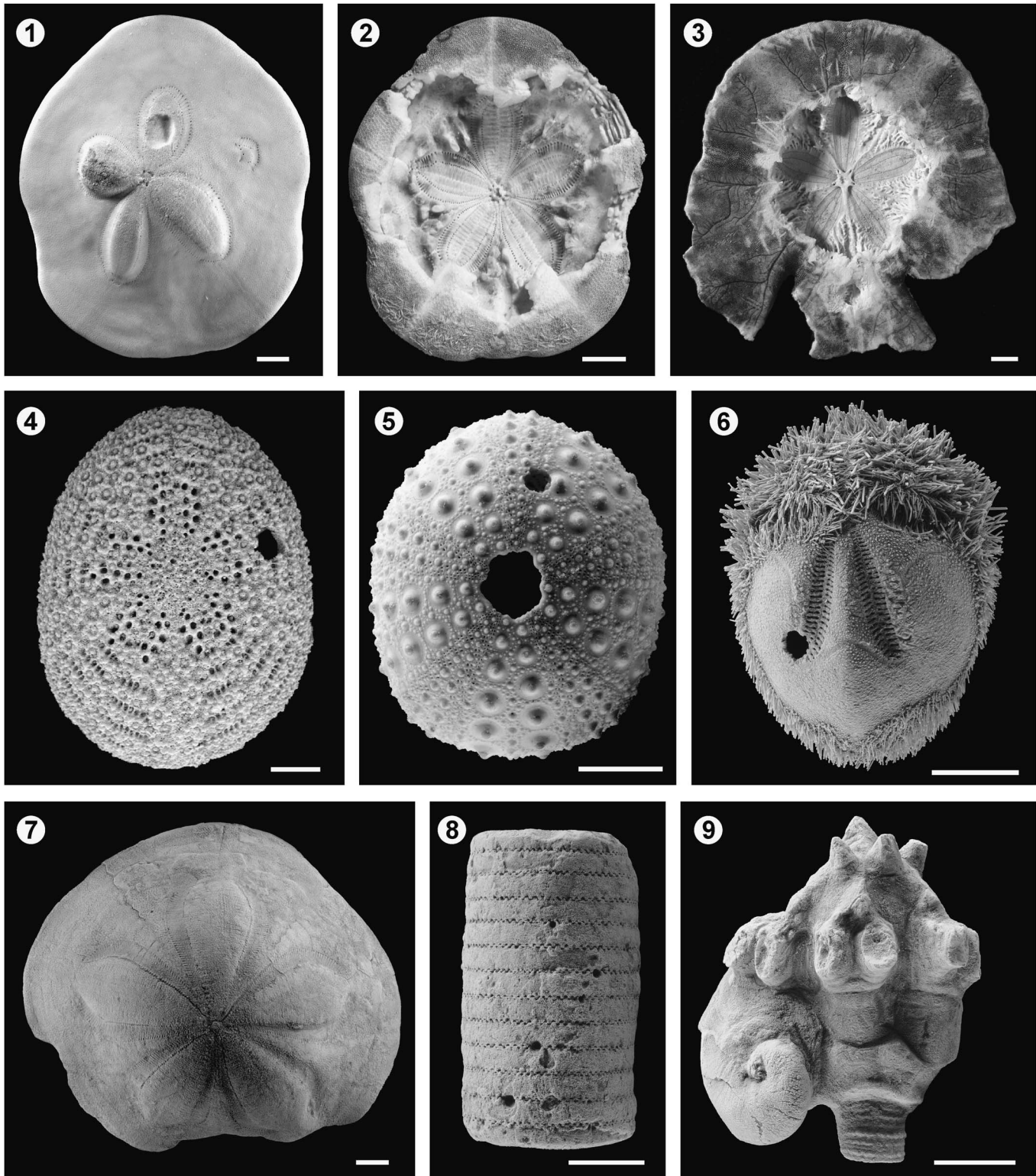
Figure 6. Traces produced on echinoderms. Predation and parasitism on clypeasteroid echinoids from the Northern bay of Safaga (Egypt, Red Sea): **(1)** *Clypeaster humulis* showing features related to sublethal predation and parasitism. The symmetry of the petalodium is totally disrupted. The left frontal petalodium is highly inflated due to a gall formation. The frontal petal shows a depression probably representing a healed gall. The right frontal petal is restricted to the distal part only. This may represent an early sublethal wound as the neighboring petals are distended in its direction; **(2)** *Clypeaster humilis* showing a massive wound on the oral surface revealing the petalodium from the inner side. Parallel scratches interpreted as tooth marks, attributed to balistid fish, are seen on the left; **(3)** *Echindoscus auritus* showing both non-lethal predation on the ambitus as well as a lethal wound at the center of the oral side of the test; **(4)** *Echinocyamus crispus* showing a clear bore hole (*Oichnus*-like) towards the upper right intersecting tubercles and ambulacral pores of the petalodium. Predation on modern echinoids from Santiago de Cuba: **(5)** *Echinometra lucunter* and **(6)** *Brissus unicolor* showing clear bore holes (*Oichnus*-like). Miocene of Valencia (E Spain): **(7)** *Clypeaster* sp. showing a very irregular ambitus, healed after crab or vertebrate predation. Parasitism on crinoids: **(8)** stem (Millericrinidae indet.) with simple pits (*Tremichnus*-like) from the Late Jurassic of the Albarracín Range (Teruel, E Spain); **(9)** *Oenochoacrinus princeps* parasitized by platyceratid gastropod from the Valporquero Formation of Colle (León, NW Spain; see Fernández-Martínez et al., 2015) (Photographs 5 to 9 are courtesy of S. Zamora). Scale bars are **(1, 2, 3, 5, 6, 7)** 1 cm; **(4)** 0.5 mm; **(8, 9)** 0.5 cm.

possible basal attachment mark left by a sessile, unmineralized invertebrate such as a sea anemone.

Arendt (2012) erected the ichnogenus *Augoichnus* to include shallow depressions, with a commonly ovoid outline, which margin is rimmed by one or two grooves, produced on the cup, brachial spines and anal sacs of early Permian crinoids (Krasnoufimsk, Russia), and also attributed its origin to the attachment of parasitic gastropods (not platyceratids).

Saint-Seine (1950, 1959) also documented several types of damage on echinoid tests (*Micraster* and *Clypeaster*) from different ages and localities, which could be attributed to the activity of parasites (maybe predators). This damage consists mainly of shallow, irregular or meandering scars or depressions produced in the outer surfaces of the tests; which in the latter case are always regenerated.

Finally, Jangoux (1990) enumerated a series of diseases that may affect echinoderms, including those produced by both micro- and macro-organisms, which may be potential producers of an ichnological record.

Traces produced by invertebrate predation on echinoderms.—It is well known that some echinoderms are active predators on a great variety of invertebrates (e.g., asterozoans; Carter, 1968), including other echinoderms (e.g., Quinn, 1965; Aronson, 1987; Baumiller et al., 2008). Echinoderms, however, are also commonly preyed upon by crustaceans, polychaetes and gastropods (e.g., Meyer and Ausich, 1983; Smith, 1984; Aronson, 1987; Baumiller and Gahn, 2003; Kowalewski and Nebelsick, 2003). Therefore, both the attacks with a fatal outcome as well as nonlethal predation can potentially produce ichnological evidence in the echinoderm skeletons.

Drilling predation (*Oichnus*-like structures) on echinoids is widely documented (Fig. 6.4–6.6); these borings are mainly attributed to the activity of cassid gastropods, although other invertebrates have been also proposed (e.g., Beu et al., 1972; Gibson and Watson, 1989; Nebelsick, 1998; Nebelsick and Kowalewski, 1999; Ceranka and Złotnik, 2003; Kowalewski and Nebelsick, 2003; Donovan and Pickerill, 2004; Grun et al., 2014; Meadows et al., 2015; Grun and Nebelsick, 2016). In fact, the ichnospecies *Oichnus halo* was erected by Neumann and Wisshak (2009) to include central holes with parallel smooth walls surrounded by one or more circular depressions. At the moment, this ichnospecies has only been described on the tests of Late Cretaceous to early Paleocene holasteroid echinoids from the northern Germany and Sweden. Based on similar traces produced by modern eulimid gastropods (genus *Thyca*) that parasitize on asteroids, Neumann and Wisshak (2009) proposed the structures generated by this group of gastropods as the modern counterpart of these trace fossils; which are interpreted to result from a combination of attachment processes and predatory feeding behavior.

Donovan and Jagt (2002, 2003, 2004, 2013) and Donovan et al. (2008) described non-penetrative *Oichnus*-like structures in Cretaceous echinoids that could be interpreted as the result of parasites or even failed predatory attacks (see Donovan, 2015 for further references). In addition, Deline (2008) documented the presence of a borehole in the Late Ordovician echinoderm *Enoploura* (Stylophora). The preservation features of these

borings may indicate a predatory origin, but parasitism is not ruled out.

Bite marks, consisting of shallow and rectilinear scratches and oval to circular pits, left by the jaw apparatus of cidaroid sea urchins on crinoid skeletons, while they feed upon, were documented by Baumiller et al. (2010) both in fossil and recent specimens.

Traces produced by vertebrate predation on echinoderms.— Today, fish are probably the most important vertebrate predators of echinoderms (e.g., Meyer and Ausich, 1983; Smith, 1984; Baumiller and Gahn, 2003; Grun, 2016), but there are others such as turtles, birds, sea otters or arctic foxes (e.g., Nebelsick, 1998; Nebelsick and Kowalewski, 1999; Kowalewski and Nebelsick, 2003; Sievers et al., 2014; and references therein).

The record of fish predation on modern and fossil crinoids and ophiuroids, is identifiable by the occurrence of regenerating arms, which in turn evidences the usual nonlethal outcome of these attacks (e.g., Meyer and Ausich, 1983; Aronson, 1987; Baumiller and Gahn, 2003, 2004; and references therein). Lethal fish attacks on clypeasteroids (see Frazer et al., 1991) leave a gaping central cavity surrounded by, in part, parallel bite marks (Nebelsick and Kampfer, 1994; Nebelsick, 1998) (Fig. 6.2, 6.3). Clypeasteroid echinoids often show evidence of bite marks along the ambitus (e.g., Vadász, 1914; Zinsmeister, 1980; Nebelsick and Kampfer, 1994; Lawrence and Vasquez, 1996; Nebelsick, 1998; Santos et al., 2003) (Fig. 6.3). These wounds can be healed since they do not reach into the central lumen of the test containing the vital organs and result in highly irregular outlines typical of sand dollars (Fig. 6.1–6.3, 6.7).

Fish tooth-marks (e.g., sharks, rays or durophagous fishes), mainly consisting of longish grooves or isolated to rowed pits or punctures, have been recognized on asterozoan ossicles (Neumann, 2000), rhabdocidaroid echinoid spines (*Linichnus*-, *Machichnus*- and *Nihilichnus*-like traces, Wilson et al., 2015; see also Donovan and Renema, 2016), and echinoid tests (Schormann, 1987). Fragmented echinoid remains can also occur as regurgitates from fish predation (Borszcz and Zatoń, 2013 and references therein).

Echinoderms as benthic islands for boring and encrusting organisms

In environments with soft muddy or sandy seafloors, the availability of hard substrates (even small, isolated and relatively stable) may be crucial for the survival of a plethora of boring and encrusting invertebrate organisms, such as barnacles, bivalves, polychaetes, sponges, or bryozoans. Encrustation during life in echinoids is restricted to the spines of cidaroids which lack the epidermis that covers most echinoids during life (David et al., 2009) or the rare encrustation of sand dollars by balanid barnacles (Merril and Hobson, 1970). Frequently, both in the fossil record and in the Recent, isolated dead echinoid tests commonly constitute benthic islands or preferential spots for the settlement and growth of these hard-substrate dwellers (Fig. 7; e.g., Nebelsick et al., 1997; Borszcz, 2012; Belaústegui et al., 2013; Borszcz et al., 2013; Rahman et al., 2015; and references therein). Additionally, modern and fossil crinoids can also be
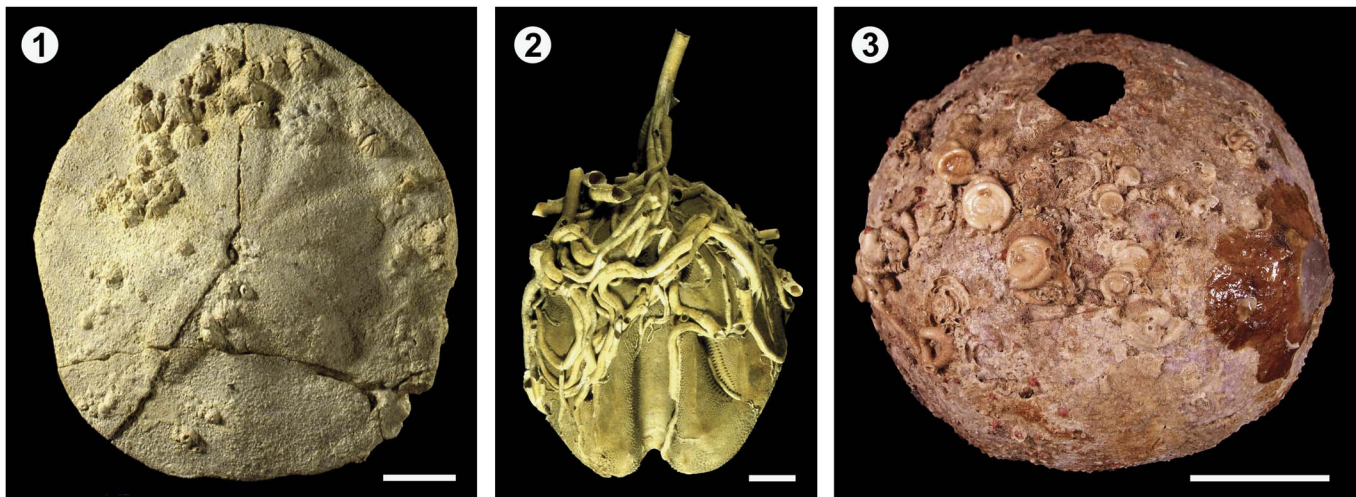
Figure 7. Echinoderms as benthic islands: **(1)** Post-mortal encrustation of the early Miocene *Clypeaster latirostris* from the Molasse Zone (Austria) by balanid barnacles; **(2)** Post-mortal encrustation of the Recent spantagoid *Ova canalifera* from the Northern Adriatic Sea by serpulid worm tubes (see Nebelsick, 2004); **(3)** Post-mortal encrustation of the Recent sea urchin *Echinus* sp. from Ibiza (Balearic Islands, Spain) mainly by bryozoans and serpulid worms. Scale bars are **(1, 2)** 1 cm; **(3)** 5 cm.

considered as benthic islands for many epidionts; in these cases the colonization may occur on both living and dead specimens (e.g., Brett and Eckert, 1982; Liddell and Brett, 1982; Peters and Bork, 1998; see also previous section concerning bioclaustrations). In addition, cystoid thecae used as benthic islands have been also documented in the fossil record (Thomka et al., 2016).

From Miocene *Clypeaster* tests deposited in a soft and non-consolidated biocalcarenite of northeastern Spain (i.e., benthic islands), Belaústegui et al. (2013) described two modes of occurrence for traces (cf. *Gastrochaenolites dijugus*) produced by gastrochaenid bivalves: (1) 'intrastereom clavate borings' restricted to the echinoid stereom; and (2) 'semi-endoskeletal dwellings', which penetrate across the test wall and extend as carbonate crypts into the sediment fill of the internal test cavity.

Jagt et al. (2009) erected the new ichnospecies *Petroxestes altera* to describe shallow, elongate borings with narrowly rounded ends and irregular bioglyphs (grooves and scratches) produced in a hemipneustid echinoid (late Maastrichtian, Belgium). Jagt et al. (2009) interpreted that this trace was produced by a sipunculid worm, after the death of the echinoid.

Conclusions

Modern and fossil bioturbation and bioerosion structures produced and interpreted as produced by echinoderms are reviewed. In the trace fossil record, 22 ichnogenera and 53 ichnospecies have been erected; among them, and following latest ichnotaxonomic discussions, 14 ichnogenera and 26 ichnospecies are considered as valid ichnotaxa. All of them correspond to bioturbation structures except four ichnogenera interpreted as bioerosion structures.

Echinoid and asterozoan traces exhibit the highest ichnodiversities both in the fossil record and today. By contrast, the ichnological record of other groups, such as crinoids or mitrates, is reduced to unique and exceptional specimens. In addition, although nowadays the different burrowing behaviors conducted by holothurians are really well known, their trace fossil record is limited at this time to a single ichnogenus and two ichnospecies.

This contribution highlights the importance of the combination of neo- and paleoichnological studies as a very powerful tool to interpret and to better understand the ecology and ethology of burrowing and boring invertebrates (echinoderms, in this particular case), and the trace fossil record.

Acknowledgments

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