

Echinoid Burrow Bichordites monastiriensis from the Oligocene of NE Italy

Authors: Bernardi, Massimo, Boschele, Sergio, Ferretti, Paolo, and Avanzini, Marco

Source: Acta Palaeontologica Polonica, 55(3): 479-486

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.0064

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Echinoid burrow *Bichordites monastiriensis* from the Oligocene of NE Italy

MASSIMO BERNARDI, SERGIO BOSCHELE, PAOLO FERRETTI, and MARCO AVANZINI



Bernardi, M., Boschele, S., Ferretti, P., and Avanzini, M. 2010. Echinoid burrow *Bichordites monastiriensis* from the Oligocene of NE Italy. *Acta Palaeontologica Polonica* 55 (3): 479–486.

Several specimens of trace fossil *Bichordites monastiriensis* were discovered in two shallow water Oligocene sandstone beds from Valsugana (Trentino, NE Italy) representing the oldest documented occurrence for this ichnospecies. They are grazing-crawling (pascichnion-repichnion) structures and are occasionally associated with enlarged structures that can be interpreted as resting traces (cubichnia) and assigned to the ichnogenus *Cardioichnus*. The resulting *Bichordites–Cardioichnus* compound trace fossil is here described for the first time. In the basal part of some specimens, skeletal remains of *Eupatagus ornatus* were found in life position. This founding enables to widen the spectrum of known *Bichordites* trace-makers. Exceptional conditions of preservation of one specimen extending in two beds recording different environmental conditions gave an opportunity to document the effects of various taphonomical histories on the preservation of this traces.

Key words: Trace fossils, Bichordites, echinoid burrows, Upogebia, foredeep, Oligocene, Italy.

Massimo Bernardi [massimo.bernardi@mtsn.tn.it], Paolo Ferretti [ferretti@mtsn.tn.it], and Marco Avanzini [avanzini @mtsn.tn.it], Museo Tridentino di Scienze Naturali, Via Calepina, 14, I-38122, Trento, Italy; Sergio Boschele [s.boschele@wwf.it], WWF Trentino- Alto Adige Südtirol, Via Malpaga 8, I-38122, Trento, Italy.

Received 4 June 2009, accepted 22 March 2010, available online 25 March 2010.

Introduction

The sedimentary succession outcropping near Borgo Valsugana, in the eastern Trento region (northern Italy) is known since the second half of 18th century (Adrian 1868; Mojsisovics 1879; Oppenheim 1902; Trener 1909; Stefanini 1915). Venzo (1940) completed the monography entitled "Studio geotettonico del Trentino meridionale-orientale tra Borgo Valsugana e Monte Coppolo" in addition with the geological map 1:25.000. Following studies by Rasplus (1963), Fuganti et al. (1965), Braga et al. (1971), Schiavinotto (1978) and, in particular, Luciani and Trevisani (1992) were focused to the Palaeogene palaeogeographic evolution of the Valsugana valley. Only Fabiani (1922a, b) and Venzo (1940, 1941) dedicated specific studies to the Valsugana fossils.

Geological setting

One of the most complete Cenozoic sedimentary successions crops out along the Ceggio creek, just little north to the village of Telve. The study of this succession undertook by one of the authors (SB) and currently ongoing is highlighting the palaeontological richness of the sedimentary units comprised between the late Eocene and the Miocene.

The hemipelagic upper Turonian Scaglia Rossa Formation is overlain (through a surface of paraconcordance) by an Upper Eocene–Upper Oligocene mixed terrigenous-carbonate

Acta Palaeontol. Pol. 55 (3): 479-486, 2010

platform succession. Priabonian calcarenitic and algal limestones (Calcare di Nago Formation) (Luciani 1989) are overlain by a composite succession comprising Oligocene algal limestones, marls and conglomerates containing a rich invertebrate fauna. Upward in the section, upper Rupelian marls and sandstones (Calcare di Linfano Formation) (Luciani and Trevisani 1992) topped by an ochre-brown surface showing karstification and iron nodules follow. The uppermost sandstones and grey-green glauconitic marls of Chattian–Aquitanian age (Monte Brione Formation) (Luciani and Trevisani 1992) close the shallow marine sedimentary succession.

The studied outcrop is located on the eastern side of the hill, between Borgo Valsugana and Telve villages, on the right side of the Ceggio Creek (Fig. 1). Beds of the Triassic–Miocene sedimentary succession that builds the hill display SSW-NNE strike and about 60° dipping to the ESE (Fabiani 1922b). The strata constitute a wide monoclinal flexure that extends westward from Telve di Sopra village, beyond the village of Olle.

The trace fossils bearing outcrop is situated on the southern side of a small valley that cuts the Oligocene sediments. The succession is locally constituted of 13 m of nodular limestones alternated with highly fossiliferous (gastropods, bivalves, echinoids, vertebrate fragments) sandy and marly beds arranged in two lithostratigraphic units, corresponding to two sedimentary parasequences (Tattesi 2006). The lower one (1) is dominated by carbonate sediments, the upper one (2) by the clastic fraction (Fig. 1).



Fig 1. Location map and stratigraphic column of the trace fossil bearing outcrop. Grey shading on the log highlights the two beds (1 and 2) bearing *Bichordites*. This study focus on bed 2.

(1) 30 cm of fine grey marly sandstones with plane-parallel lamination.

Dark carbonate pebbles millimeter-sized are scattered in the sediment along with plant remains and small limonitized pyrite nodules. In these beds internal moulds of gastropods (Naticidae and Cassidae) and bivalves (Veneeriidae, Crassatellidae) and, close to the top, fragments of chelonids and fish scales, have been documented. At the top the clay marly fraction decreases and is substituted by the arenaceous one.

(2) 150 cm of yellow sandstones beds with plane-parallel lamination.

Plant remains related to continental flora are abundant. Among invertebrates, echinoids (*Eupatagus*), gastropods (mainly naticids) and bivalves (pectinids) are well represented at the top. Pectinids and echinoids are well preserved, whereas the other fauna is found, mostly, as internal mould. These beds host scattered skeletal remains referable to the Sirenia. At the top, an erosive surface marks the contact with a grey conglomerate with carbonatic matrix and centimetre-sized well sorted and rounded carbonatic and metamorphic pebbles.

Palaeoenvironmental interpretation

The described beds represent the top of a decimetric shallowing-coarsening upward sequence.

A thick marly bed at the base is overlain by several coarsening upward sandy layers. This sequence is interpreted as a progressive shallowing from a fully marine to a shallow water coastal environment. Invertebrate faunal association is coherent with a shallow marginal marine environment. The basal level (1) presents very high H_2S and organic matter contents

BERNARDI ET AL.-OLIGOCENE ECHINOID BURROW

that are coherent with a poorly oxygenated lagoonal environment. The passage to the overlaying arenaceous bed (2) is marked by a colour change. The fine-grained grey-black layer (1) is overlain by yellow-red sandstones (2) interpreted as deposited in a well oxygenated coastal environment. The increased concentration of centimetre-sized plant and vertebrate (Sirenia) remains indicate proximity to the coastline supporting the reconstruction for this area of a low depth fluviomarine mixing zone. The conglomerate that overlies these sequences probably represents a wide fluvial delta lobe with sediments eroded from the lifting alpine ridge situated northward, and transported into the "Valsugana basin". At the top of the conglomerate a red surface of pedogenised sandstones testify the emersion of the area, as observed by Venzo (1940).

The spatangoids

The order Spatangoida Agassiz, 1840 (Echinodermata: Echinoidea) comprises numerous families of fossil and extant benthic deposit feeders. Spatangoids are one of the echinoid groups with the best fossil record (Kier 1977). The earliest members appeared at the base of the Cretaceous and diversified in continental shelf clastic settings. Skeletal remains indicate that during the Late Cretaceous and Tertiary more families diverged and spatangoids expanded into chalk seas (Fischer 1966; Smith 1984) although trace fossil evidences document an earlier migration of irregular echinoids to the deep sea in the latest Jurassic (Tithonian; see Tchoumatchenco and Uchman 2001).

Most spatangoids live infaunally and some have evolved deep burrowing capabilities, unique example among echinoids (Seilacher 2007), in order to better exploit organic detritus when feeding (Kroh 2007). Spatangoids are "key-bioturbators" (Bromley et al. 1997) of modern marine environments and a similar importance has been suggested also for past ecosystems (e.g., Uchman 1995, 2001, 2007). Spatangoid burrowing mechanisms are well known; studies have been conducted both on trace fossils and living forms whose behaviour is accepted as a good analogue for past strategies (e.g., Nichols 1959; Howard et al. 1974; Bromley and Asgaard 1975; Bromley et al. 1997).

All spatangoids possess dense aboral spines and aboral respiratory tube feet; deep burrowers, or those living in fine sediment, use their adapical tube-feet in the frontal ambulacrum to maintain a duct that permit constant contact with the surface (Smith 1984). Their plastron is armed with two sets of stout spines which push the sediment backwards and provide the principal thrust for forward locomotion (Smith and Crimes 1983). Most spatangoids, at least for part of their life, present highly specialised structures that played a central role in the evolution of infaunality (Néraudeau et al. 1998): the fascioles. These are specialised bands of small, densely packed spines known as clavulae that bear enlarged bulbous tips containing mucous glands. Fascioles are important in generating water circulation through the burrow and to produce a sheet of mucous that is used to compact the burrow margins (Smith 1984).

Spatangoids produce distinct traces that have been identified in the global fossil record (e.g., Smith and Crimes 1983; Noda 1985; Plaziat and Mahmoudi 1988; Mayoral and Muñiz 2001; Gibert and Goldring 2008); they are however not common as could be expected, probably because of preservational issues (Goldring and Stephenson 1970; Bromley and Asgaard 1975).

The existence of modern spatangoids exhibiting grazing and burrowing behaviours similar to those recorded in the fossil record enables confident attribution of trace fossils to their most probable producer.

Several ichnogenera have so far been attributed to spatangoids; known traces record grazing-crawling behaviour (pascichnia-repichnia, e.g., *Bichordites*, *Scolicia*), and resting behaviour (cubichnia, e.g., *Cardioichnus*). In addition, the vertical trace of the funnel used for respiratory purposes has been assigned to the ichnogenus *Monocraterion* (Plaziat and Mahmoudi 1988; but see Jensen 1997).

Nomenclatural issues

In several, successive, publications various interpretations have been proposed by different authors for the ichnotaxonomic attribution of the traces described herein. In this paper we adopted the widely accepted nomenclature proposed by Uchman (1995, 1998). Uchman proposed that large meniscate burrows with evidence of the presence of a single drain should be assigned to Bichordites, while those with evidence of two sanitary tubes should be assigned to Scolicia independently of their preservational features. Furthermore he proposed to include the ichnogenera Laminites Ghent and Henderson, 1966, Subphyllochorda Götzinger and Becker, 1932, Taphrhelminthopsis Sacco, 1888, and Taphrhelminthoida Książkiewicz, 1977 within the ichnogenus Scolicia de Quatrefages, 1849 as taphonomic variants of the same ichnogenus (see Bertling et al. 2006 for a discussion). Uchman (1995, 1998) suggestions are contrary to the original Plaziat and Mahmoudi (1988) proposals that called Laminites the full-relief burrow produced by the spatangoid ploughing in the substrate, while Bichordites was limited to the central part of the burrow. In the same paper the negative epireliefs of the Laminites structure were attributed to Scolicia, while the positive hyporeliefs were subdivided in Subphyllochorda and Taphrhelminthopsis.

Trace fossils attributable to spatangoids sensu lato

A full-relief core-like trace was found to cross the stratigraphic boundary between the red sandstones (2) and the underlying grey marly sandstones (1) (Fig. 2A, B). The whole trace fossil



Fig. 2. Trace fossil *Bichordites* from the Oligocene of Valsugana (Trentino, NE Italy) showing the effects of the different taphonomic histories of beds (1) and (2). **A**. Full-relief. **B**. Schematic interpretation of the trace. **C**. Detail of the central core. **D**. Detail of the meniscate laminae. **E**. Transverse section of the burrow.

(total length ~40 cm) is an extremely well preserved full-relief burrow deepening at an angle of about 30° with the palaeosurface. The section of the trace fossil extending in the upper beds (2) is a bipartite to flattened rod (average width 0.7 cm) constituted by a fine brown sediment (Fig. 2C). A transverse section shows a little black round spot in the lower-medial part of the rod; this correspond to a small tube (diameter ~0.1 cm) that runs within the rod for all its length. This section of the trace terminates upwards with an enlargement (diameter 2.5 cm); the opposite end correspond to the base of the red sandstone bed. The trace shows all the characters that enable confident assignation to *Bichordites monastiriensis* Plaziat and Mahmoudi, 1988 (Uchman 1995). Here *Bichordites* is represented by a well cemented rod that surrounds a single drainage canal (also known as sanitary tube) left by the echinoid burrowing in the substrate. It is constituted by the sediment that has been reworked with the mucus produced by the fascioles and shaped by the presence of a tuft of long spines around the anus (Plaziat and Mahmoudi 1988; but see Schlirf 2002). The inner little dark tube corresponds to the true drainage channel

BERNARDI ET AL.-OLIGOCENE ECHINOID BURROW



Fig. 3. Spatangoid burrow from the Oligocene of Valsugana. A. Inferred behaviour of the trace maker. B. Taphonomic controlled preservation of the burrow and resulting traces. C. Schematic interpretation of the relations between the described trace fossils.

filled by a string of faecal material. Below, within the grey marly sandstone the trace fossil continues with a lower inclination (~20° with respect to the palaeosurface), but here an external layer of red sandstone showing clear proximally convex meniscate laminae (average width 4 cm; Fig. 2D) covers the rod. *Bichordites* is here preserved in all its components. It presents a concentric, layered structure typical of this ichnogenus; notably, the cross section of Fig. 2E, is remarkably similar to that shown in D'Alessandro and Uchman (2007: fig. 4B). The outer layer is constituted by the sediment backfilling structures of the burrow that are accumulated while the an2imal is ploughing into the sediment. This is formed by successive parallel lamellae that take the shape of the posterior part of the echinoid (see also Seilacher 2007: 78). The inner layer is the continuation of the previously described rod.

The particular crossing-bed position of the described trace fossil provides a unique instance for the examination of the effects of different environments of preservation on the taphonomic history of the same original structure. The presence of a reductive environment (grey marly sandstones) has permitted the preservation of the whole burrow, even of the poorly cemented backfill meniscate laminae. From the base of the red sandstone, deposited in oxygen rich waters, the laminated sediment of the burrow was probably rapidly reworked. Here, only the stout mucus-bounded grains have been preserved (Fig. 3). The central core is known to be preferentially better preserved due to heavy impregnation (e.g., Nara 2004).

Several other full-relief core-like trace fossils (diameters from 1 to 5 cm) extending parallel or weakly oblique to the sediment laminations have been found within the red sandstone beds (2) (Fig. 4). They can be traced for a decimetric to metric distance. Transverse section is weakly bilobate but no internal rod is visible. These traces cannot therefore be attributed with confidence to any ichnogenus; however their general external shape is remarkably *Bichordites*-like.

Trace fossils attributable to *Eupatagus ornatus*

Several sub-cylindrical full-relief burrows with average diameter of 2.5 cm were found in the upper beds of the yellow sandstone (Fig. 5A) of layer (2). Burrows are filled by the same sediment constituting the surrounding matrix. All the trace fossils present similar morphology and are recognisable



Fig. 4. Full-relief *Bichordites*-like trace fossils from the Oligocene of Valsugana (Trentino, NE Italy) extending for metric distances. **A**. Several traces run weakly oblique with respect to the palaeosurface. **B**. Other traces are parallel to the stratification.



Fig. 5. Compound trace fossils *Bichordites–Cardioichnus* from the Oligocene of Valsugana (Trentino, NE Italy). **A**. Photograph. **B**. Schematic interpretation. **C**. Eupatagus ornatus (Defrance in Brongiart 1822) found at the end of the trace.

only because of their orange-brown colour, which probably resulted from the oxidation of the sediment with increased concentration in organic matter (e.g., mucus) accumulated by the backfilling activity of the tracemaker. All traces are cut by the outcrop surface along a longitudinal section.

After a first steep, nearly vertical, interval (~13 cm) the trace fossils progressively gently curve and end horizontally (~12 cm). Running within each trace fossil a single, vain, core-like structure of ~0.5 cm is visible. This feature allows attribution of the trace fossil to *Bichordites monastiriensis*. Some of them intergrade with ovoid enlargements showing two symmetrical lateral lobes. These are found at regular intervals of about 10 cm along the burrow. These enlargements, expanding in all sides from the burrow axis, highly resemble the resting trace (cubichnion) *Cardioichnus* Smith and Crimes, 1983. *Cardioichnus* however also extends downward and displays bilobate lower side that in the here described material is

not visible due to the longitudinal orientation of the traces with respect to the outcrop surface. It is probable that the trace maker was successively ploughing through the sediment, resting and then ploughing again and so on (Fig. 5B). As a result, a compound *Bichordites–Cardioichnus* trace fossil originated (see Pickerill and Narbonne 1995 for a review). The association of these trace fossils is here documented for the first time. At the end of some traces, skeletal fragments of *Eupatagus ornatus* (Defrance in Brongniart 1822) were found preserved in life position (Fig. 5C). At the end of few other traces, echinoid skeletal remains were so poorly preserved that it has not been possible to determine them. However the general shape of the remains and the low echinoid diversity found in the surrounding sediment strongly point towards *Eupatagus* as unique producer of the traces.

Discussion

Bichordites is known to be produced by spatangoids that belong to the Echinocardium group (Plaziat and Mahmoudi 1988). This has also been proved by Broomley and Asgaard (1975) that reported Echinocardium cordatum in life position at the end of Bichordites traces. These echinoids typically present one tuft of subanal spines that produce a single drain channel. Conversely, the producers of Scolicia are known to belong to the Spatangus group that, bearing two tufts of spines, produce two drain channels (cf. Smith and Crimes 1983; Uchman 1995). Asgaard and Bromley (2007) considered the family Echinocardiidae to be unique in having a single tuft, however Gibert and Goldring (2008) suggested Maretia (family Maretiidae) as the likely producer of the Bichordites traces found in the Bateig Limestone (see also Gibert and Goldring 2007). We can asses with confidence that the spatangioids found in association with the here described Bichordites traces were found in life position. The echinoids perished at end of the burrows that they were excavating and there were found with the tests "mouth down" as expected; furthermore the trace fossil bearing sediment is not disturbed apart from the described Bichordites-Cardioichnus compound traces.

Having found several specimens of *Eupatagus ornatus* (family Maretiidae) we provide support to the Gibert and Goldring (2008) findings. We therefore suggest to widen the spectrum of the producers for the *Bichordites* trace in order to comprise both the Echinocardiidae and the Maretiidae.

The oldest *Bichordites monastiriensis* so far documented are those reported by Uchman and Krenmayr (1995) and Uchman (1995) respectively in the Miocene of Austria and Italy. The here documented occurrence in the Oligocene sediments of Valsugana is thus the oldest for *Bichordites*.

Trace fossils attributed to sea urchins are commonly found in deep-sea turbidites (e.g., Colella and D'Alessandro 1988; Gibert and Goldring 2008) suggesting a good ability of these organisms to overcome even catastrophic events. Ex-

BERNARDI ET AL.-OLIGOCENE ECHINOID BURROW

periments conducted on modern echinoids seems to confirm this ability (e.g., Rodrigues et al. 2001). We can therefore confidentially rule out sediment drowning as killing mechanism. Stratigraphy of the outcrop, as described in the above section, is consistent with a palaeoenvironmental transition from a fully marine setting to a near shore environment highly influenced by terrestrial hydrography. Echinoids are known to be extremely sensitive to salinity fluctuations (stenohaline condition). Even considering that salinity variations are attenuated in interstitial waters (Johnson 1967), a rapid variation of the surrounding waters from normal marine to brackish can be considered as a possible killing mechanism.

Conclusions

Several specimens of the trace fossil Bichordites monastiriensis were discovered in a shallow water Oligocene coastal deposits. This founding represent the oldest for this ichnogenus. Grazing-crawling trace fossils are locally associated with resting traces assigned to the ichnogenus Cardioichnus; The resulting Bichordites-Cardioichnus compound trace fossil is here documented for the first time. Exceptional conditions of preservation of one Bichordites specimen extending in two beds deposited in very different environments gave the opportunity to clearly document the effects of various taphonomical histories on trace fossil preservation. An anoxic taphonomic environment permits the preservation of the whole Bichordites burrow even in its most fleeting, poorly cemented backfilling structures (the meniscate laminae). Conversely, in an oxygen rich sediment only the mucus-bounded central core is preserved.

Several maretiids, assigned to *Eupatagus ornatus*, were found in life position in association with *Bichordites*. The inclusion of the Maretiidae family, together with the already known Echinocardiidae, as producers of *Bichordites* traces is proposed.

Acknowledgements

The manuscript was improved by the helpful comments of Andrea Baucon (Geopark Naturtejo Meseta Meridional, Idanha-a-Nova, Portugal) and Fabio Massimo Petti (Museo Tridentino di Scienze Naturali, Trento, Italy). We are indebted to Alfred Uchman (Jagiellonian University, Kraków, Poland) and an anonymous reviewer for their constructive comments and for improvement of the language. We also thank Jarosław Stolarski for help and assistance during editing process. The present paper derives from the collaboration of the authors: MB has collected the specimens, elaborated the data and written the manuscript with the cooperation of MA, SB has discovered the site and determined the faunas, PF has collaborated in the collection of specimens and geological data. This study was supported by the Museo Tridentino di Scienze Naturali (Trento, Italy) and, for MB, by the Italian Presidency of the Council of Ministers—UNSC.

References

- Asgaard, U. and Bromley, R.G. 2007. Co-occurrence of schizasterid echinoids and the trace fossil *Scolicia*, Pleistocene, Greece: facts, myths and fascioles. *In*: R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise, and R.N. Melchor (eds.), Sediment—Organism Interactions: A Multifaceted Ichnology. *Society of Economic Palentologists and Mineralogists (Society for Sedimentary Geology) Special Publications* 88: 87–95.
- Adrian, F. 1868. Neogenschichten aus dem Pissavacca-Thal und Coalba-Thal bei Strigno in Südtirol. Verhandlungen der kaiserlich-königlichen geologischen Reichsanstalt 3: 1–5.
- Agassiz, L. 1840. Catalogus systematicus ectyporum echinodermatum fossilium Musei Neocomensis. 20 pp. O. Petitpierre, Neuchâtel.
- Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikuláš, R., Nielsen, J.K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M., and Uchman, A. 2006. Names for trace fossils: a uniform approach. *Lethaia* 39: 265–286. http://dx.doi.org/10.1080/00241160600787890
- Braga, G., Gatto, G.O., Gatto, P., Gregnanin, A., Massari, F., Medizza, F., Nardin, M., Perna, G., Rossi, D., Sacerdoti, M., Semenza, E., Sommavilla, E., Zirpoli, G., and Zulian, T. 1971. Note Illustrative della Carta Geologica d'Italia, Foglio n. 22 "Feltre", sc. 1:100.000. 150 pp. Servizio Geologico Italiano, Roma.
- Bromley, R.G. and Asgaard, U. 1975. Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bulletin of the Geological Society of Denmark* 24: 261–281.
- Bromley, R.G., Asgaard, U., and Jensen, M. 1997. Experimental study of sediment structures created by a spatangoid echinoid, *Echinocardium mediterraneum*. Proceedings of the Geologists' Association 108: 183–189.
- Brongniart A. 1822. Sur quelques terrains de craie hors du Bassin de Paris. In: G. Cuvier and A. Brongniart (eds.), Recherches sur les ossemens fossiles. Nouvelle Édition 2 (IIe), 316–337. Dufour et d'Ocagne, Paris.
- Colella, A. and D'Alessandro, A. 1988. Sand waves, *Echinocardium* traces and their bathyal depositional setting (Monte Torre Palaeostrait, Plio-Pleistocene, southern Italy). *Sedimentology* 35: 219–237. http://dx.doi.org/10.1111/j.1365-3091.1988.tb00946.x
- D'Alessandro, A. and Uchman, A. 2007. Bichordites and Bichordites-Rosselia ichnoassemblages from the Lower Pleistocene Tursi Sandstone (southern Italy). In: R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise, and R.N. Melchor (eds.), Sediment—Organism Interactions: A Multifaceted Ichnology. Society of Economic Palentologists and Mineralogists (Society for Sedimentary Geology) Special Publications 88: 213–221.
- Fabiani, R. 1922a. Il Terziario nel Trentino. Memorie dell'Istituto Geologico della Reale Università di Padova 6: 1–60.
- Fabiani, R. 1922b. Continuità della serie fra Oligocene e il Miocene nel Trentino meridionale. Atti dell'Accademia Scientifica Veneto-Trentino-Istriana, Classe di Scienze Naturali, Fisiche e Matematiche 12–13: 119–122.
- Fischer, A.G. 1966. Spatangoids. In: R.C. Moore (ed.), Treatise on Invertebrate Paleontology, Part U, Echinodermata 3, 543–547. Geological Society of America and University of Kansas Press, Boulder, Colorado.
- Fuganti, A., Morteani, G., and Ungaro, S. 1965. Studio sedimentologico e micropaleontologico dei sedimenti terziari di Castel Tesino (Trento) con riferimento al tettonismo del "cristallino di Cima d'Asta". *Studi Trentini di Scienze Naturali* 17: 274–300.
- Ghent, E.D., and Henderson, R.A. 1966. Petrology, sedimentation and paleontology of Middle Miocene graded sandstone and mudstone, Kaiti Beach, Gisborne. *Transactions of the Royal Society of New Zealand*, *Geology* 4: 147–169.
- Gibert, J.M. and Goldring, R. 2007. An ichnofabric approach to the depositional interpretation of the intensely burrowed Bateig Limestone, Miocene, SE Spain. *Sedimentary Geology* 194: 1–16. http://dx.doi.org/10.1016/j.sedgeo.2006.04.008
- Gibert, J.M. and Goldring, R. 2008. Spatangoid-produced ichnofabrics (Bateig Limestone, Miocene, Spain) and the preservation of spatangoid trace fos-

sils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 270: 299–310. http://dx.doi.org/10.1016/j.palaeo.2008.01.031

- Goldring, R. and Stephenson, D.G. 1970. Did Micraster burrow? Geological Journal Special Issue 3: 179–184.
- Götzinger, G. and Becker, H. 1932. Zur geologischen Gliederung des Wienerwaldflysches (Neue Fossilfunde). Jahrbuch der Geologische Bundesanstalt 82: 368–380.
- Howard, J.D., Reineck, H.E., and Rietschel, S. 1974. Biogenic sedimentary structures formed by heart urchins. *Senckenbergiana Maritima* 6: 185–205.
- Jensen, S. 1997. Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. Fossils and Strata 42: 1–111.
- Johnson, R.G. 1967. Salinity of interstitial water in a sandy beach. *Limnology* and Oceanography 12: 1–7. http://dx.doi.org/10.4319/lo.1967.12.1.0001
- Kier, P.M. 1977. The poor fossil record of the regular echinoid. *Paleobiology* 3: 168–174.
- Kroh, A. 2007. *Hemipatagus*, a misinterpreted Loveniid (Echinodermata: Echinoidea). *Journal of Systematic Palaeontology* 5: 163–192. http://dx.doi.org/10.1017/S1477201906002021
- Książkiewicz, M. 1977. Trace fossils in the flysch of the Polish Carpathians. Palaeontologia Polonica 36: 1–208.
- Luciani, V. 1989. Stratigrafia sequenziale del Terziario nella catena del monte Baldo (Province di Verona e Trento). *Memorie di Scienze Geologiche* 41: 263–351.
- Luciani, V. and Trevisani, E. 1992. Evoluzione paleogeografica del Paleogene della Valsugana. Annali dell'Università di Ferrara, sezione Scienze della Terra 3: 83–99.
- Mayoral, E. and Muñiz, F. 2001. New ichnospecies of *Cardioichnus* from the Miocene of the Guadalquivir Basin, Huelva, Spain. *Ichnos* 8: 69–76. http://dx.doi.org/10.1080/10420940109380174
- Mojsisovic, E. 1879. Die Dolomit-Riffe von Südtirol und Venetien: Beiträge zur Bildungsgeschichte der Alpen. 551 pp. A. Holder Verlag, Wien.
- Nara, M. 2004. Trace fossil *Bichordites monastiriensis* in Pleistocene shallow marine deposits of the Boso Peninsula, central Japan, and its paleoenvironmental significance. *Journal of the Geological Society of Japan* 110: 19–20.
- Néraudeau, D., David, B., and Madon, C. 1998. Tuberculation in spatangoid fascioles: Delineating plausible homologies. *Lethaia* 31: 323–334.
- Nichols, D. 1959. Changes in the chalk heart-urchin *Micraster* interpreted in relation to living forms. *Philosophical Transactions of the Royal Society of London (B)* 242: 347–437. http://dx.doi.org/10.1098/rstb.1959.0007
- Noda, H. 1985. Miocene and Pliocene spatangoid echinoid burrows from Okinawa and Chiba Prefectures, Japan. *Annual Reports of the Institute of Geosciences of the University of Tsukuba* 11: 41–44.
- Oppenheim, P. 1902. Revision der tertiären Echiniden Venetiens und Trentino. Der Zeitschrift der Deutschen Geologischen Gesellschaft 54: 159–283.
- Pickerill, R.K. and Narbonne, G.M. 1995. Composite and compound ichnotaxa: a case example from the Ordovician of Quebec, eastern Canada. *Ichnos* 4: 53–69. http://dx.doi.org/10.1080/10420949509380114
- Plaziat , J.-C. and Mahmoudi, M. 1988. Trace fossils attributed to burrowing echinoids: a revision including new ichnogenus and ichnospecies. *Geobios* 21: 209–233. http://dx.doi.org/10.1016/S0016-6995(88)80019-6
- Quatrefages, M.A. de 1849. Note sur la Scolicia prisca (A. De Q.) annélide fossile de la craie. Annales des Sciences Naturelles, série 3, Zoologie 12: 265–266.

- Rasplus, L. 1963. Etude gèologiche de la region de Castello-Tesino (Alpes-Méridionales, province de Trente, Italie). Bulletin de la Société géologique de France, Series 7a 5: 790–797.
- Rodrigues, N., Sharma, R., and Nath, B.N. 2001. Impact of benthic disturbance on megafauna in Central Indian Basin. *Deep-Sea Research II* 48: 3411–3426. http://dx.doi.org/10.1016/S0967-0645(01)00049-2
- Sacco, F. 1888. Note di paleoichnologia italiana. Atti della Società Italiana di Scienze Naturali 31: 151–192.
- Schiavinotto, F. 1978. Nephrolepidina nella valle del Maso (Borgo Valsugana – Italia settentrionale). Rivista Italiana di Paleontologia 84: 729–750.
- Schlirf, M. 2002. Taxonomic reassessment of *Bolonia* Meunier, 1886 (trace fossil) based on new material from the type area in Boulonnais, northern France. *Paläontologische Zeitschrift* 76: 331–338.
- Seilacher, A. 2007. *Trace Fossil Analysis*. 226 pp. Springer-Verlag, New York.
- Smith, A.B. 1984. *Echinoid Palaeobiology*. 190 pp. Allen and Unwin, London.
- Smith, A.B. and Crimes, T.P. 1983. Trace fossils formed by heart urchins—a study of *Scolicia* and related traces. *Lethaia* 16: 79–92. http://dx.doi.org/10.1111/j.1502-3931.1983.tb01147.x
- Stefanini, G. 1915. Il Neogene del Veneto. *Memorie dell'Istituto Geologico della Reale Università di Padova* 3: 337–624.
- Tattesi, B. 2006. Associazioni a Vertebrati Fossili del Terziario della Valsugana (Trento): considerazioni stratigrafiche e paleoecologiche. 180 pp. Unpublished M.Sc. thesis, Department of Earth Sciences, University of Padova, Italy.
- Tchoumatchenco, P. and Uchman, A. 2001. The oldest deep-sea Ophiomorpha and Scolicia and associated trace fossils from the Upper Jurassic–Lower Cretaceous deep-water turbidite deposits of SW Bulgaria. Palaeogeography, Palaeoclimatology, Palaeoecology 169: 85–99. http://dx.doi.org/10.1016/S0031-0182(01)00218-8
- Trener, G.B. 1909. Geologische Spezialkarte der Österreichischen Monarchie. Blatt Borgo-Fiera di Primiero, Scala 1:25.000. Geologischen Reichsanstalt, Wien.
- Uchman, A. 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria* 15: 1–115.
- Uchman, A. 1998. Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material. *Annales Societatis Geologorum Poloniae* 68: 105–218.
- Uchman, A. 2001. Eocene flysch trace fossils from the Hecho Group of the Pyrenees, northern Spain. *Beringeria* 28: 3–41.
- Uchman, A. 2007. Deep-sea ichnology: development of major concepts. *In*:W. III Miller (ed.), *Trace Fossils Concepts, Problems, Prospects*, 248–267. Elsevier, Amsterdam.
- Uchman, A. and Krenmayr, H.G. 1995. Trace fossils fom lower Miocene (Ottnangian) molasse deposits of Upper Austria. *Paläontologische Zeitschrift* 69: 503–524.
- Venzo, S. 1940. Studio geotettonico del Trentino meridionale-orientale tra Borgo Valsugana e M. Coppolo. Memorie dell'Istituto Geologico dell' Università di Padova 14: 5–86.
- Venzo, S. 1941. Fossili oligocenici della Valle del Maso (Valsugana). *Studi Trentini di Scienze Naturali* 22: 173–210.