

Unusual echinoid resting trace records change in the position of the redox boundary (Palaeogene of the Lesser Caucasus in Georgia)

ALFRED UCHMAN¹, ZURAB LEBANIDZE², NINO KOBAKHIDZE³, TAMAR BERIDZE³,
DAVIT MAKADZE⁴, KOBALOBZHANIDZE³, SOPHIO KHUTSISHVILI³, RUSUDAN CHAGELISHVILI⁵,
KAKHA KOIAVA² and NINO KHUNDADZE⁴

¹ Faculty of Geography and Geology, Institute of Geological Sciences, Jagiellonian University, Gronostajowa 3a, 30-387 Kraków, Poland. E-mail: alfred.uchman@uj.edu.pl

² Department of Geology, Faculty of Exact and Natural Sciences, Iv. Javakishvili Tbilisi State University, University str. 13, 0186 Tbilisi, Georgia. E-mails: zurab.lebanidze@tsu.ge; kakha.koiava@tsu.ge

³ Alexander Janelidze Institute of Geology, Iv. Javakishvili Tbilisi State University, Politkovskaia 31, 0186 Tbilisi, Georgia. E-mails: ninokobakhidze88@gmail.com; tamara_beridze@yahoo.com; tamrikoberidze1969@gmail.com; koba.lobzhanidze@gmail.com; sofio.sofiko@gmail.com

⁴ Alexander Tvalchrelidze Caucasian Institute of Mineral Resources, Tbilisi State University, 12 Mindeli str., 0186 Tbilisi, Georgia. E-mails: maqadze9292@gmail.com; n.khundadze@gmail.com.

⁵ Department of Geology and Paleontology, Georgian National Museum, 3 Purtseladze str., 0105 Tbilisi, Georgia. E-mail: rchagelishvili@gmail.com.

ABSTRACT:

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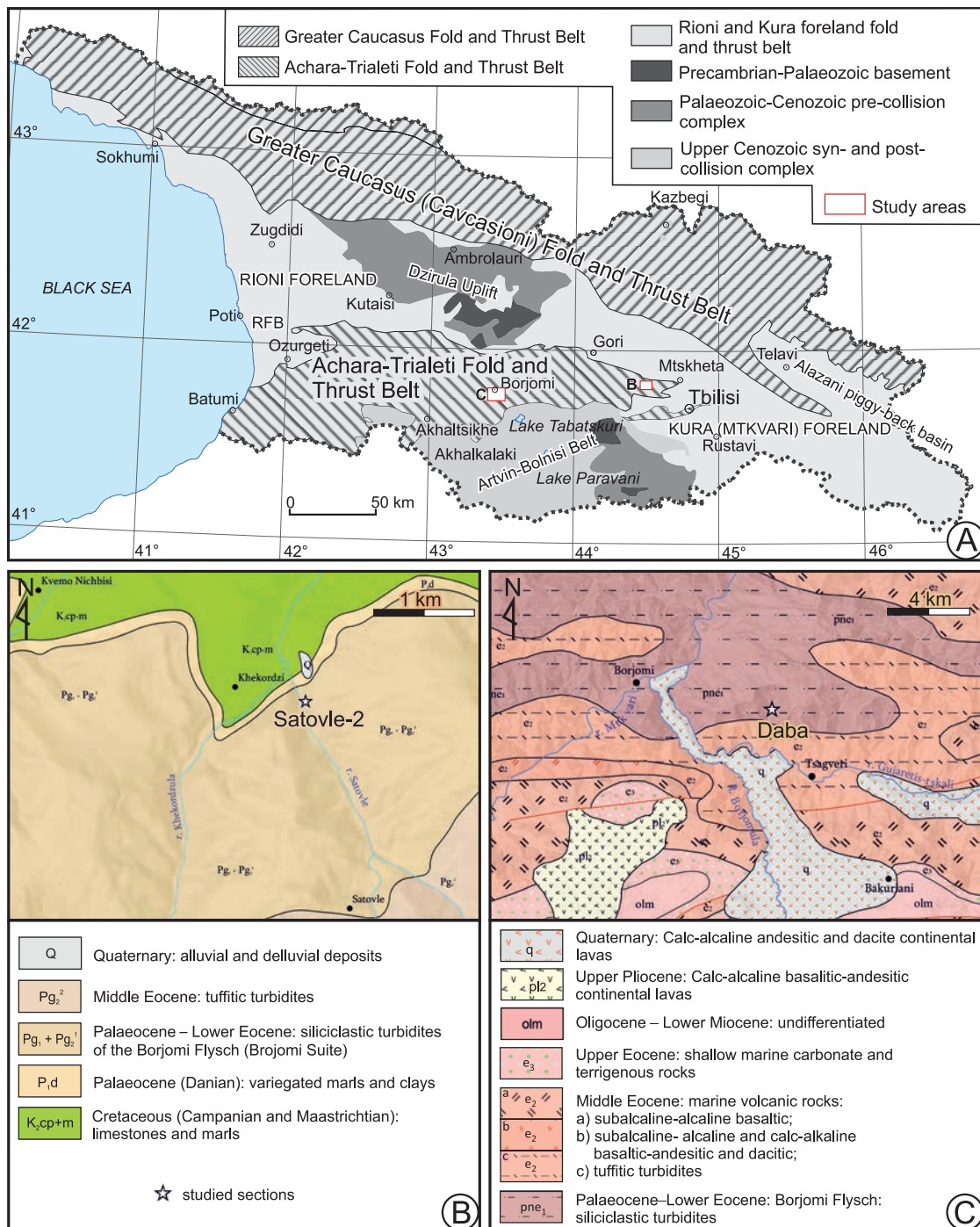
The first recognition of a tracemaker responding to a temporary shift in the redox boundary is recognized. This is recorded by a new trace fossil, *Sursumichnus orbicularis* igen. et isp. nov., which is established for mound-like structures on the upper surfaces of sandstone beds from the Borjomi Flysch (upper Paleocene–lower Eocene) in the Lesser Caucasus (Georgia). It is connected with the spatangoid echinoid burrow *Scolicia* de Quatrefages, 1849 and interpreted as a resting trace of the same tracemaker produced after moving up from a deeper position within the sediment. The resting is caused by an episode of unfavourable conditions related to shallowing of the redox boundary. The trace fossil is a component of the *Nereites* ichnofacies.

Key words: Ichnotaxonomy; New ichnotaxa; Irregular echinoids; Deep sea; Flysch; Redox boundary; Oxygenation.

INTRODUCTION

Resting traces (ethological category cubichnia) record a relatively long stay of an animal in one place in the sediment without burrowing action (Seilacher 1953). Among them, the trace fossil *Cardioichnus* Smith and Crimes, 1983 is usually preserved as a

hypichnial bilobate mound on sandstone beds. It is interpreted as a trace of irregular echinoids, which remained in place within the sediment at a greater depth than the usually associated locomotion/feeding trace leading there (e.g., Mayoral and Muñiz, 2001; Brustur 2005; Naimi *et al.* 2021). Thus, the echinoid moved deeper to rest. An unusual trace



Text-fig. 1. Location maps. A – Map of Georgia, with indication of the main geological units and the study area (based on Adamia *et al.* 2011a). B – Map of the Satovle-2 section area (based on Papava 1966). C – Map of the Borjomi area, with indication of the Daba section (based on Adamia 2004).

fossil of similar nature occurs in Palaeogene deposits of the Lesser Caucasus, which indicates that the tracemaking echinoid moved to a shallower position for resting. We are not aware of any literature per-

taining to such behaviour. Description of this trace fossil, an appropriate decision on its ichnotaxonomy, classification and its interpretation are the main aims of this paper.

GEOLOGICAL SETTING AND LOCALITIES

The Achara-Trialeti Fold-and-Thrust Belt (ATFTB) is located in the frontal part of the Lesser Caucasus orogen, extending in a 45–65 km-wide belt for 360 km along strike from the Black Sea coast towards Tbilisi (Text-fig. 1; Adamia *et al.* 2002). The eastern ATFTB plunges under the fill of the Kura Basin south-east of Tbilisi. The ATFTB resulted from the structural inversion of a deformed back-arc rift-basin fill; the basin was the likely eastward prolongation of the eastern Black Sea, which opened in Cretaceous–Eocene times (Adamia *et al.* 2011b; Sosson *et al.* 2016). The present-day geometry of the ATFTB is related to the northward thrusting of the basement wedge(s) and developed from the middle or late Miocene to the Pleistocene (Banks *et al.* 1997; Alania *et al.* 2017; Corrado *et al.* 2021; Gusmeo *et al.* 2021). The ATFTB is composed of syn-rift (Cretaceous–upper Eocene), post-rift (Oligocene–lower Miocene) megasequences, and synorogenic strata (middle Miocene–Pleistocene). The stratigraphic relationships are disturbed by extensional to compressional complex phases of tectonism since the Cretaceous (Alania *et al.* 2021).

The study area includes the central segment and the frontal part of the eastern part of the ATFTB. The Borjomi area (central segment) is typical of the Paleocene–lower Eocene Borjomi Flysch, which is also called the Borjomi Suite (Text-fig. 2). The Borjomi Suite is subdivided into the Tusrebi, Boshuri and Bolevani subsuites (Beradze *et al.* 1985). The Palaeocene (Thanetian) Tusrebi Subsuite constitutes nearly three-quarters (900–1000 m) of the entire thickness of the Borjomi Flysch. Recently, it was subdivided into three lithofacies units: 1) the lower Tusrebi shaly unit, composed of packages of often marly mudstones, siltstones and very fine-grained sandstones, 2) the sand-rich middle Tusrebi unit, consisting of sandy packages separated by shaly intercalations, and 3) the upper Tusrebi shaly unit (Uchman *et al.* 2020). The volcanogenic-sedimentary Boshuri Subsuite contains deformed (slumped) deposits rich in volcanic material and related debris-flow deposits, graded sandstones (typical turbidites), and amalgamated massive sandstones interbedded with mudstones and siltstones. In some cases, thick intervals of amalgamated sandstones consist of thin intercalations of locally laminated mudstone or siltstone. Some silty laminae mark amalgamation surfaces. The mainly shaly Bolevani Subsuite terminates the Borjomi Suite and is formed by deep-sea heterolithic deposits (sandstones with thin alternations of pelagic and hemipelagic mudstones and siltstones). The latter two members are dated to the early Eocene

(Ypresian). The Borjomi Suite is conformably overlain by approximately 2000–3000 m thick middle Eocene volcanic and volcanogenic deposits. According to previous studies, the Borjomi Flysch was deposited under shallow-marine and hemipelagic conditions (Yilmaz *et al.* 2001). However, recent interpretations point to a deep-sea environment (Lebanidze *et al.* 2017; Uchman *et al.* 2020; Beridze *et al.* 2021; this paper).

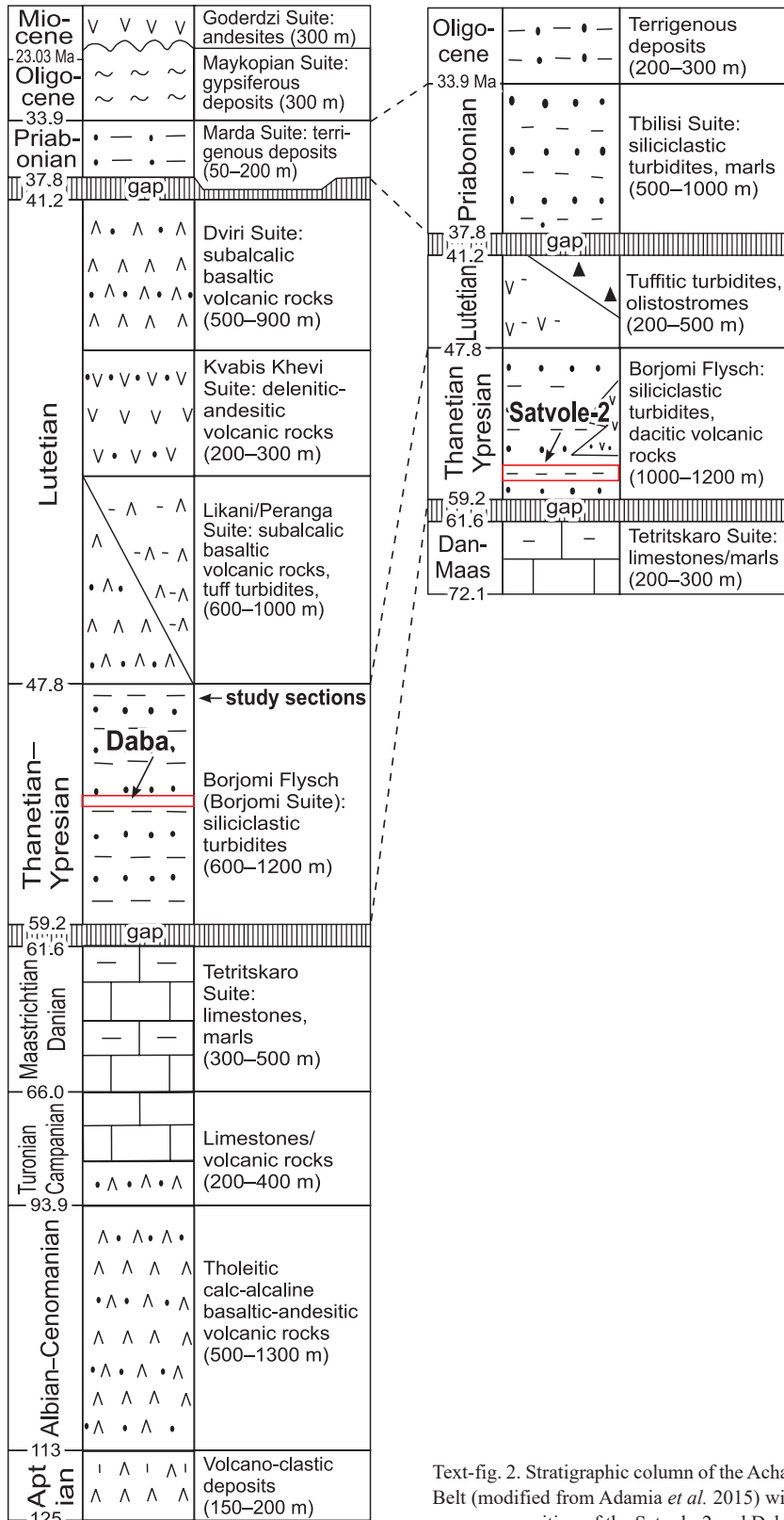
Upper Cretaceous limestones, marls, sandstones, mudstones, and siltstones, 600–1800 m thick, are the oldest deposits of the eastern part of ATFTB. Here, the Palaeocene is represented by 50 to 450 m thick shales, marls, turbidites, and the lower Eocene by 500 to 1000 m thick conglomerates, mudstone-siltstone shales, turbiditic sandstones, and volcanic dacite. The middle Eocene volcanogenic-sedimentary strata (debrites, sandstone turbidites) and mudstone-siltstone shales, which are 300–800 m thick, and the upper Eocene conglomerates, mudstone-siltstone shales, and sandstone turbidites, which are 400–800 m thick, represent younger strata (Papava 1967; Banks *et al.* 1997; Adamia *et al.* 2002, 2011a; Beridze 2019; Alania *et al.* 2020). The 900 to 1100 m thick Palaeocene–lower Eocene turbiditic deposits are distinguished as the Borjomi Suite. They rest conformably on biostratigraphically dated Danian variegated marls (Papava *et al.* 1971) and extend in a continuous belt along the northern slope of the Trialeti Range.

The Satovle-2 section (Text-fig. 1B; GPS: 41°49' 20.1''N; 44°33'58.3''E) is located in the River Kura Basin, in the eastern part of the ATFTB, 5.5 km southwest of the Dzegvi railway station, in the gorge of the Satovle river, which is a right-bank tributary of the river Khekordzula that in turn represents a right-bank tributary of the Kura river. The section is located in the southern limb of the Mtskheta (Armazi) Anticline (dip azimuth 145°; dip angle 15°) and is composed of Palaeocene deposits of the Borjomi Suite.

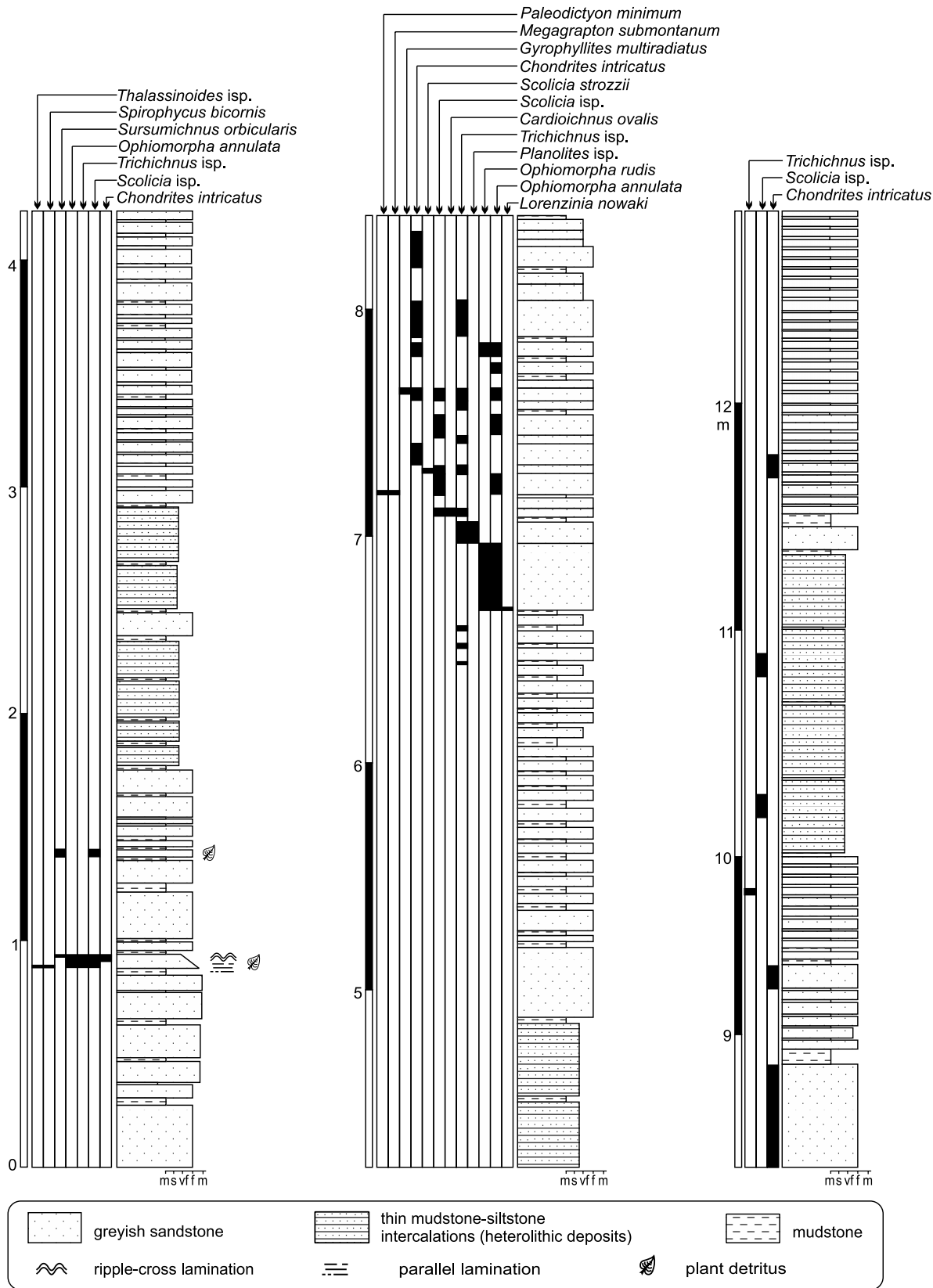
The Satovle-2 section, 13.5 m thick, consists mainly of thin- and medium-bedded fine-grained calcareous sandstones alternating with mudstones, in which sandstones are dominant (Text-fig. 3). The sandstones are very thinly (2–2.5 cm) to thinly (3–10 cm) and medium-bedded (10–29 cm). Most of the mudstones are 0.2–1 cm thick. In the middle and upper parts of the section, very thin-bedded fine-grained sandstones are also present. Some sandstone beds from the lower part of the section show T_{abc} Bouma intervals. The section shows an overall thinning-upward trend and an increase in the bioturbation degree. The studied trace fossil occurs in the lower part of the section in two levels: (1) at the top of a 14 cm thick bed of very grey, parallel and ripple-cross laminated,

Central part

Eastern part



Text-fig. 2. Stratigraphic column of the Achara-Trialeti Fold-Thrust Belt (modified from Adamia *et al.* 2015) with indication of the position of the Satvle-2 and Daba sections.



Text-fig. 3. The Satovle-2 section with indicated trace fossils.

fine- to fine-grained calcareous sandstone capped by a grey mudstone a few cm thick, and (2) at the top of a 3–5 cm thick grey fine-grained sandstone bed, which contains carbonized plant detritus. The two beds are separated vertically by 50 cm.

The Daba section (Text-fig. 1C; GPS: 41°49'27.9"N; 43°27'26.37"E; dip azimuth 175°; dip angle 45–50°) is located on the steep, southern flank of the Borjomi Anticline, in the environs of Daba village, in the gorge of river Dabiskhevi (right-bank tributary to the river Gujarula), approximately 5.5 km southeast of Borjomi Central Park and 4 km east of the Ardagani 1 section described by Uchman *et al.* (2020). The Daba section belongs to the uppermost part of the lower Tusrebi Suite, which is dated to the upper Palaeocene (Thanetian) on the basis of microforaminifera (Beradze *et al.* 1985; Mrevlishvili 2003); it is coeval with the Ardagani-1 section of Uchman *et al.* (2020).

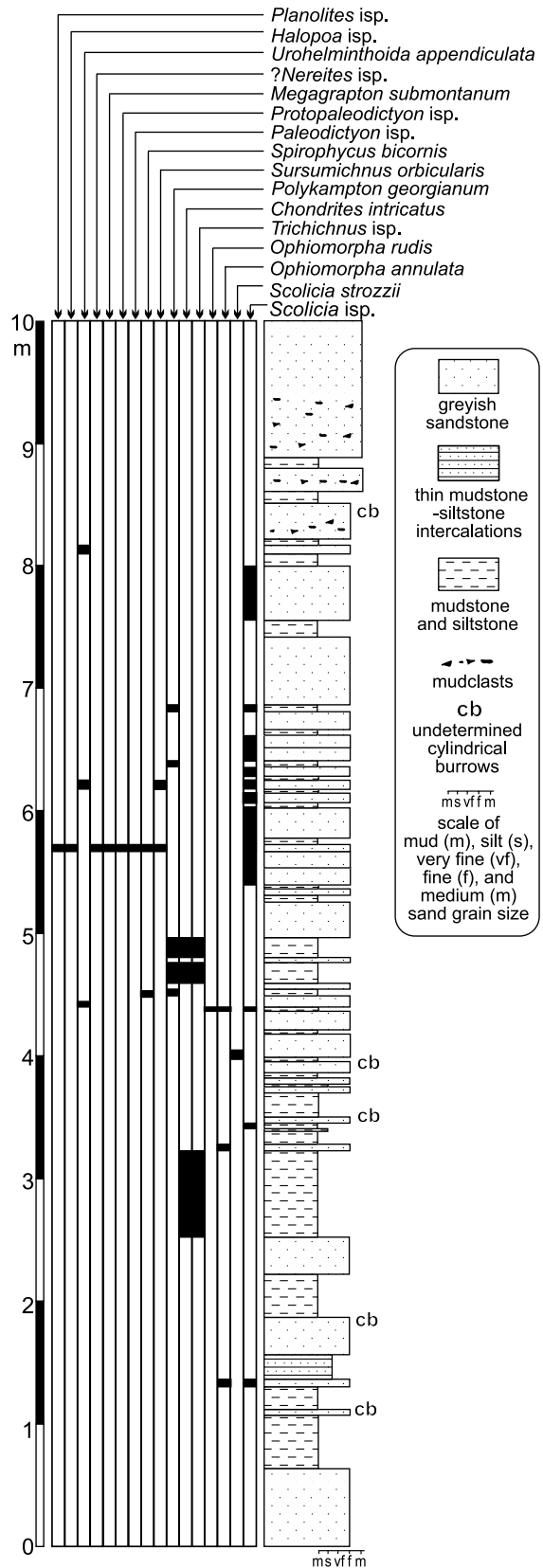
The Daba section exposes 10 m of light grey, fine- to medium-grained calcareous sandstones and mudstones with rare intercalations of siltstones (Text-fig. 4). They form sandstone-mudstone and sandstone-mudstone-siltstone packages, which are 2–4 m thick. The mudstones are light grey and fissile. They form 2–15 cm, exceptionally 40–70 cm thick beds. The 5–30 cm, or rarely 46–70 cm thick sandstone beds are parallel or wavy/convolute laminated and crossed by calcite-filled fractures. Single 1–2 cm thick siltstone beds occur in the middle part of the section. In the lower part of the section, thick-bedded mudstones predominate. In the middle and upper part of the section, the mudstone beds are thinner while sandstone beds are thicker. These sandstones are medium-grained and often contain mudclasts. The section shows an overall coarsening- and thickening-upwards trend; in the upper part of the section the sand content increases. The described trace fossil occurs in the lower part of the section at the top of a 6 cm thick bed of fine-grained calcareous sandstone and at the top of the 8 cm thick bed of fine-grained calcareous sandstone. The beds are separated stratigraphically by 42 cm.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Sursumichnus* igen. nov.

TYPE ICHNOSPECIES: *Sursumichnus orbicularis* isp. nov., by monotypy.

DIAGNOSIS: Epichnial, circular, subcircular, ovate or oval, low discoid mound, which can be slightly bilobate and have a marginal sinus.



Text-fig. 4. The Daba section with indicated trace fossils.

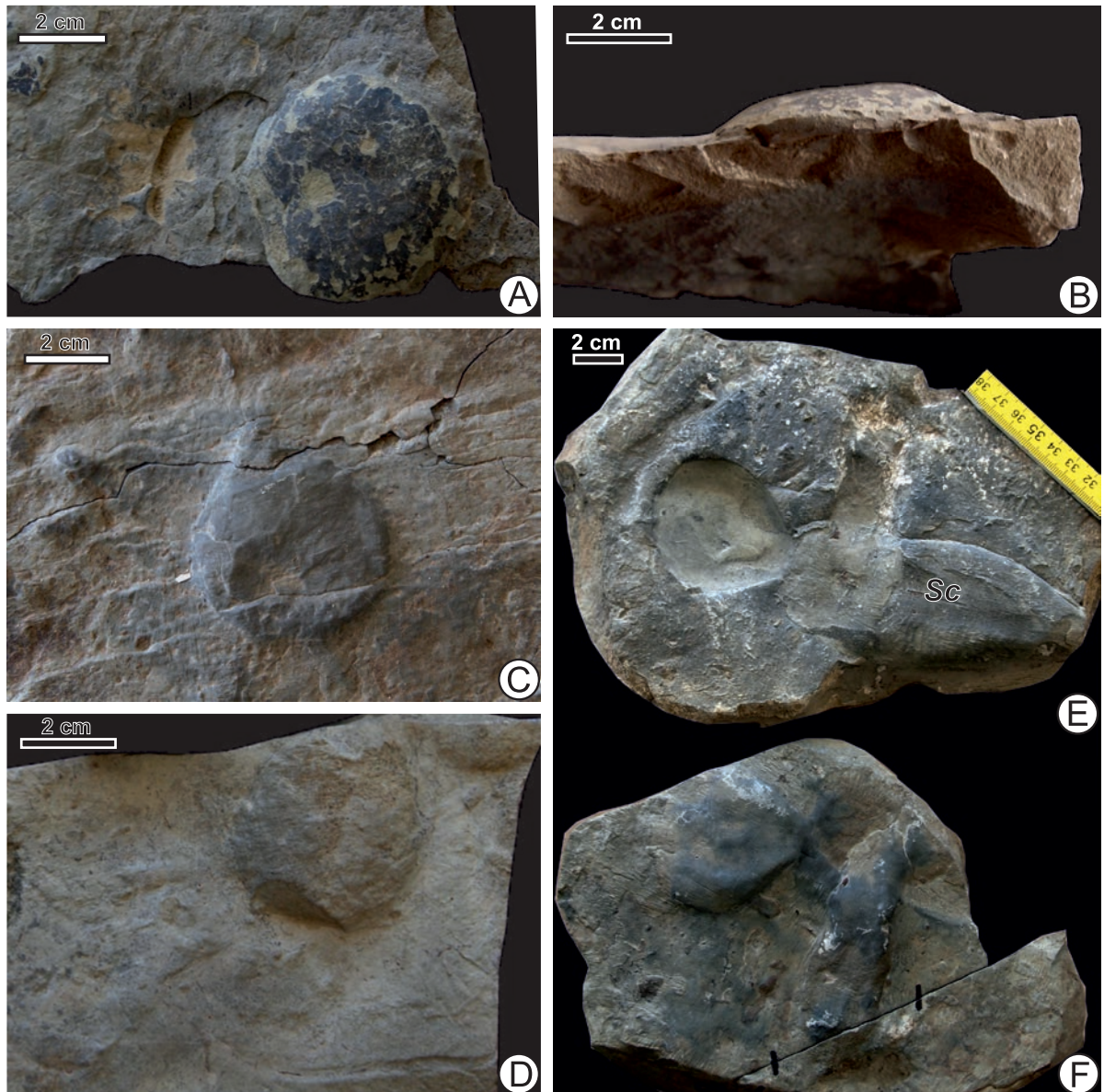
DERIVATION OF NAME: From Latin *sursum*, meaning up, above or upwards, and from Latinized Greek ἵχνοϛ (*ichnos*), meaning trace.

REMARKS: One might consider the possibility that the specimens assigned to *Sursumichnus* igen. nov. represent an ichnospecies of *Cardioichnus*, but all five ichnospecies of the latter are hypichnial bilobate mounds (see Naimi *et al.* 2021) and the ichnospecies consistency would be spoiled by inclusion of epichnial mounds. Other epichnial mound-like

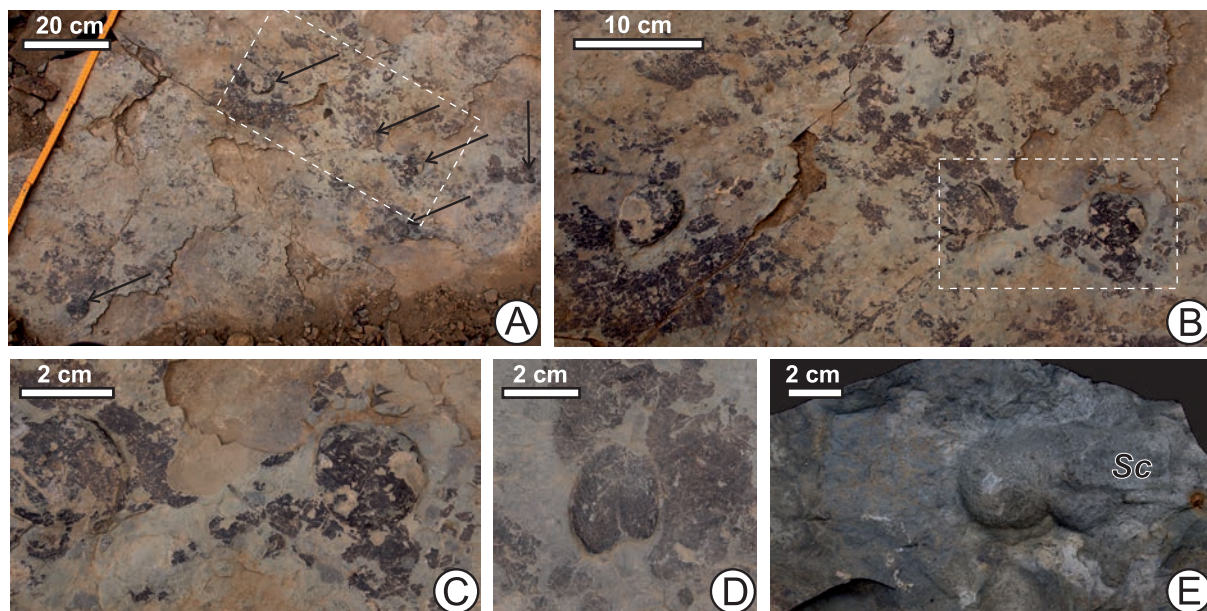
ichnogenera are different. *Chomatichnus* Donaldson and Simpson, 1962 is a crater-like structure composed of faecal strings and pierced by a central shaft (Häntzschel 1975).

Sursumichnus orbicularis isp. nov.
(Text-figs 5–7)

TYPES AND OTHER MATERIAL: Holotype – TSU01TF00090 (Satovle-2 section; Text-fig. 5A, B). TSU01TF00061a, b (Daba section; Text-fig. 5E, F),



Text-fig. 5. *Sursumichnus orbicularis* igen. et isp. nov. from the Borjomi Suite. A, B – Holotype, TSU01TF00090, Satovle-2 section; A – upper surface of bed, B – side view. C – Paratype, TSU01TF00060, Daba section. D – TSU01TF00093, Satovle-2 section. E, F – TSU01TF00061a, b, Daba section, E – base of the overlying bed, which is a counterpart of the specimen in F (*Sc* – *Scolicia* isp.), F – top of bed, counterpart of specimen in E.



Text-fig. 6. *Sursumichnus orbicularis* igen. et isp. nov. in field photographs from the Satovle-2 section. A – Upper bedding plane with *S. orbicularis* indicated by arrows. The quadrangle shows portion illustrated in B. B – Detail of A. The quadrangle shows the portion illustrated in C. C – Detail of B. D – Atypical specimen, indicated by vertical arrow in A. E – Top of siltstone-mudstone bed with *Scolicia* (*Sc*) terminated by poorly developed *S. orbicularis*.

TSU01TF00060 (Daba section; Text-fig. 5C), which is the paratype, TSU01TF00092 (Satovle-2 section; Text-fig. 6), TSU01TF00093 (Satovle-2 section; Text-fig. 5D), and photographs of seven other specimens left in the field (Text-fig. 6).

REPOSITORY: The illustrated specimens are housed in the Department of Geology of the Faculty of Exact and Natural Sciences at the Iv. Javakhishvili Tbilisi State University, Tbilisi, Georgia (institutional abbreviation TSU01TF).

TYPE LOCALITY: Satovle-2 section (Text-figs 1B and 3; GPS: 41°49'20.1"N; 44°33'58.3"E).

TYPE HORIZON: Borjomi Suite (Palaeocene–lower Eocene) (Text-fig. 2).

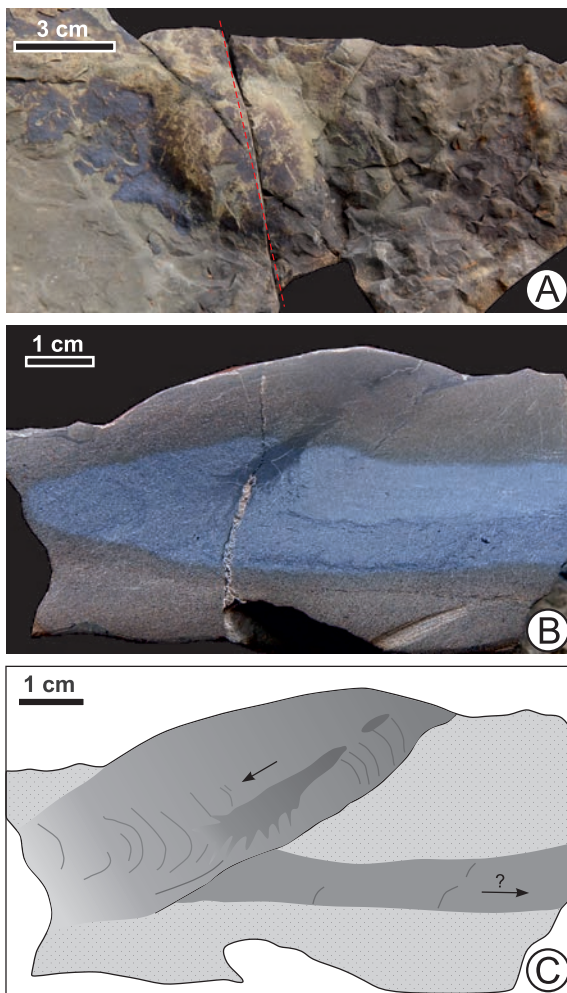
DERIVATION OF NAME: From Latin *orbicularis*, meaning circular, in correspondence to the prevailing overall shape.

DIAGNOSIS: Subcircular or ovate mound that may be bilobate and show a sinus on the margin on the prolongation of an axial depression separating the lobes.

DESCRIPTION: The holotype (Text-fig. 5A, B) is an epichnial, low, subcircular mound, gently elevated

with a central apex. It is slightly bilobate. The lobes are separated by a wide and shallow, median furrow, which is deeper at one side, becomes shallower toward the other end and disappears at the distance of about one quarter width from the mound margin. On the deeper side, the margin of the mound shows a wide shallow sinus, so the overall outline of the mound is slightly heart-shaped. The lobes are up to 49 mm long. The width measured perpendicular to the median furrow reaches 52 mm. The width measured along the median furrow is 46 mm. The mound displays a slope of about 40°. The top is nearly flat. The apex is located shortly behind the prolongation of the median furrow, it. The height of the mound in this part reaches 10 mm. The surface of the mound is smooth and most of it is covered with a dark grey patina that is probably composed of manganese oxides and hydroxides. The mound's margin is bordered off from the host bed by a discontinuity along the edge of the specimen (Text-fig. 5B).

Specimen TSU01TF00061 (parts a and b) is ovate in outline, 65 mm long and 60 mm wide. Its marginal part (part a; Text-fig. 5F) is elevated and forms a low rim that encircles a shallow, flat-bottomed depression. The depression shows a small, flat-topped elevation in the middle that is 15 mm long and 10 mm wide. The structure is complemented by a counterpart (part b; Text-fig. 5E) preserved as a depression



Text-fig. 7. *Sursumichnus orbicularis* igen. et isp. nov., TSU01TF 00092, Borjomi Suite, Satovle-2 section. A – Upper surface of bed; red dashed line marking the direction of cross-section shown in B and C. B – Cross-section; polished and wet surface. C – Interpretative drawing of B. Two burrows in grey shade. Arrows show direction of movement of the tracemaker.

on the lower surface of the overlying bed. The morphological elements of the depression mirror these from part a of the specimen being its negative casts. The depression is accompanied with *Scolicia* isp. (52 mm wide) preserved in full relief, which terminates on its margin. Its position is slightly lower than the depression.

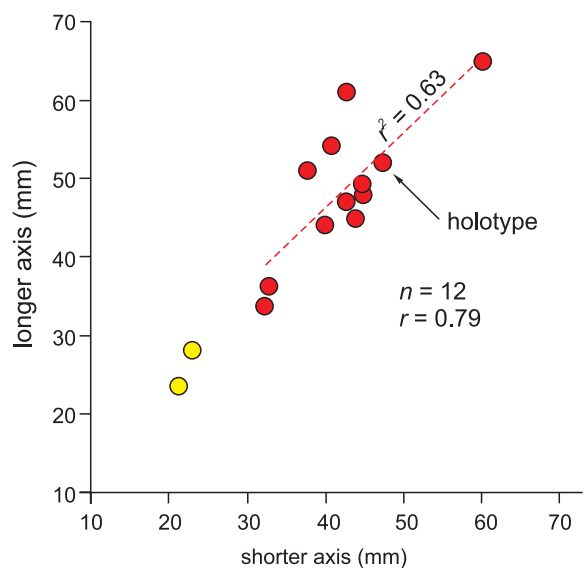
Specimen TSU01TF00092 has been cross-sectioned (Text-fig. 7). The cross-section shows an oblique structure with arcuate lithological heterogeneities and a discontinuous central core. Concavities of the arcs face to reverse direction to the mound. The discontinuity between the mound and the host bed is

visible only on the margin of the mound for a distance of a few millimetres. The remaining part is welded with the bed.

Some specimens (Text-figs 5C, 7A) are associated with a centimetre-wide, low, indistinct ridge which runs from the margin of the mound and disappears at some distance. Most specimens do not show the median depression or the sinus at the margin (Text-fig. 6A–C). Margins of some specimens are overhanging. Significantly, one of the specimens observed in the field in the Satovle-2 section occurs as a terminus of *Scolicia* de Quatrefages, 1849 (Text-fig. 6E).

For twelve measured specimens, the longer axis of the mound ranges from 34 to 65 mm (mean 48.8 mm), and the axis perpendicular to it from 32.5 to 60 mm (mean 42.8 mm). The proportions between the measured distances are relatively constant (Text-fig. 8). The coefficients of correlation ($r = 0.78$) and determination ($r^2 = 0.62$) of these parameters are high.

Two specimens observed in the Satovle-2 section on the same bedding plane with the typical *Sursumichnus orbicularis* igen. et isp. nov. are distinctly smaller, 23×21 mm and 29×22 mm. They are distinctly bilobate, with a median furrow, deeper and wider at the side of the sinus, and shallower and narrower toward the opposite end (the larger specimen in Text-fig. 6D). They lie in the same size trend as the typical *S. orbicularis* igen. et isp. nov. (Text-fig. 8), and so are included in the same ichnotaxon (*S. cf. orbicularis*) with reservation.



Text-fig. 8. Length of long and short axes of *Sursumichnus orbicularis* igen. et isp. nov. The two points in yellow refer to the small specimens, which are reservedly included in *S. orbicularis*.

REMARKS: The overhangs on the margins of the mounds are manifested as discontinuities resulting from small overthrustings of sand pushed upward along the upper bedding plane. The pressure was caused by the tracemaker and resistance from the overlying sediment and water. The concavity of the arcs below the mound (Text-fig. 7) indicates that the tracemaker moved obliquely downward into the sediment. No evidence of the burrowing action is seen above the mounds in all specimens.

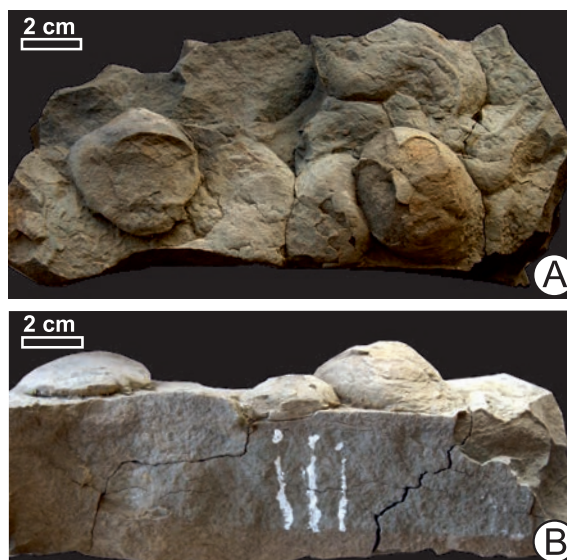
ASSOCIATED TRACE FOSSILS

In the Satovle-2 section (Text-fig. 3), *Sursumichnus orbicularis* igen. et isp. nov. co-occurs with *Scolicia* isp., *Ophiomorpha annulata* (Książkiewicz, 1977), *Chondrites intricatus* (Brongniart, 1923), *Trichichnus* isp., *Spirophycus bicornis* (Heer, 1877), and *Thalassinoides* isp. In other beds of the Satovle-2 section, *Gyrophyllites multiradiatus* (Heer, 1877), *Trichichnus* isp., *Scolicia strozzii* (Savi and Meneghini, 1850), *Scolicia* isp., *Thalassinoides* isp., *Helminthopsis* isp., *Cardioichnus ovalis* Smith and Crimes, 1983 (Text-fig. 9), *Lorenzina nowaki* (Książkiewicz, 1970), *Megagraption submontanum* (Azpeitia Moros, 1933) and *Paleodictyon minimum* Sacco, 1888 are present. *Helminthopsis* isp., *?Helminthorhapha* isp., and the tubular macroforaminifer *Bathysiphon* sp. have been found there in debris.

At the Daba section, *Sursumichnus orbicularis* igen. et isp. nov. co-occurs with *Scolicia* isp., *Helminthorhapha* isp., *Paleodictyon maximum* (Eichwald, 1868), *Spirophycus ?bicornis*, *Nereites* isp., *Protopaleodictyon* isp., and *Megagraption submontanum*. In other beds (Text-fig. 4), *Helminthorhapha* isp., *Megagraption submontanum*, *Protopaleodictyon* isp., *Paleodictyon* isp., *Spirorhapha* isp., *?Nereites* isp., *Spirophycus bicornis*, *Polykampton georgianum* Uchman, Lebanidze, Beridze, Kobakhidze, Lobzhanidze, Khutsishvili, Chagelishvili, Makadze, Koiava and Khundadze, 2020, *Chondrites intricatus*, *Trichichnus* isp., and *Ophiomorpha* isp. are present. *Capodistria vetersi* Vialov, 1968, *Zoophycos* isp., *Urohelinthoida appendiculata* (Heer, 1877), and *Megagraption irregulare* Książkiewicz, 1968 have been found there in debris.

DISCUSSION

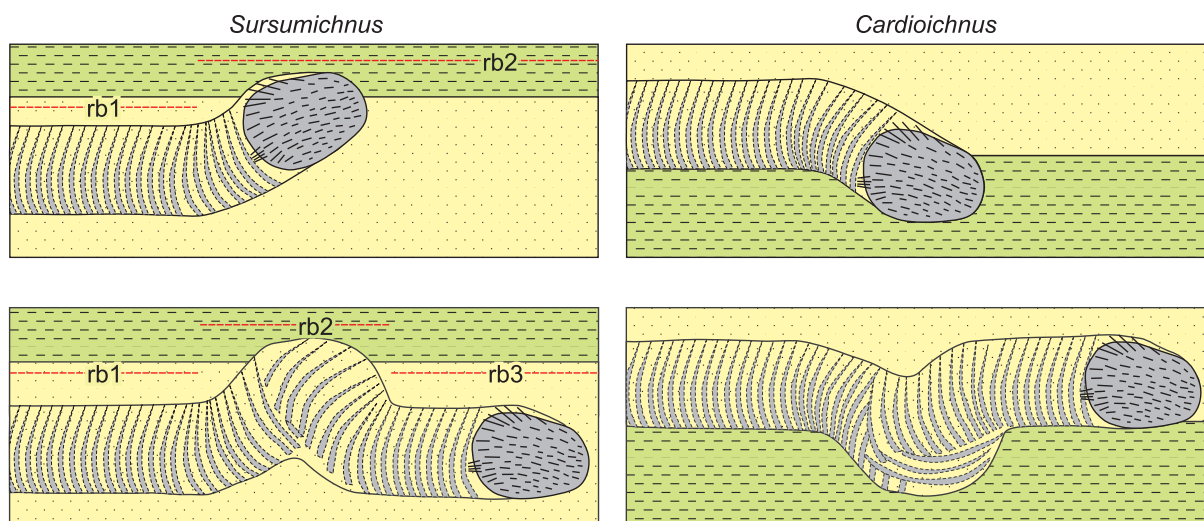
The specimen of *Sursumichnus orbicularis* igen. et isp. nov. that occurs as a prolongation of *Scolicia*



Text-fig. 9. Hypichnial *Cardioichnus ovalis* Smith and Crimes, 1983 from the lower part of Borjomi Suite, Satovle-2 section, TSU01TF00091. A – lower bedding plane. B – side view.

proves that these trace fossils have the same tracemaker. *Scolicia* as well as *Cardioichnus* are well determined as burrows of irregular spatangoid echinoids (Bromley and Asgaard 1975; Smith and Crimes 1983); however, the association of some *Cardioichnus* with *Bichordites* Plaziat and Mahmoudi, 1988 suggests that burrowing echinoids of the *Echinocardium* Gray, 1825 group, the main producers of *Bichordites*, can produce *Cardioichnus* as well (Bernardi et al. 2010). All these relationships prove that *Sursumichnus* igen. nov. is a trace of burrowing irregular echinoids. Its more or less isometric shape, similar to *Cardioichnus*, suggests the same nature of the trace, implying a resting trace. The principal difference between these two ichnogenera is that the tracemaker of *Cardioichnus* moved downward within the sediment (Smith and Crimes 1983), whereas the tracemaker of *Sursumichnus* igen. nov. moved upward in it.

The resting traces belong to the ethological category cubichnia (Seilacher 1953, 2007). They are produced for many purposes (Bromley 1996; O'Brien et al. 2009; Kopaska-Merkel and Rindsberg 2016), usually for hiding against predators, ambushing prey (Seilacher 1964; Bromley 1996; Buatois and Mángano 2012), avoiding dehydration (Martin 2006), or waiting out temporarily unfavourable environmental conditions (Kopaska-Merkel and Rindsberg 2016). Why did the burrowing echinoids move upward in the sediment for resting? Hiding against predators is excluded because the animal moved to a shallower, not deeper



Text-fig. 10. Scheme of *Sursumichnus* igen. nov. formation compared with *Cardioichnus* Smith and Crimes, 1983. The model of *Cardioichnus* formation is inspired by Smith and Crimes (1983). Dashed lines labelled with rb1, rb2, rb3 indicate successive position of redox boundary.

position in the sediment. The ambush of prey is excluded as well because they were not predators but sediment feeders. Among unfavourable environmental conditions, the change of salinity or change of oxygenation can be taken in account. It is known that echinoids are mostly stenohaline animals that poorly tolerate salinity fluctuations (e.g., Russell 2013). It is possible that less saline waters could be introduced by hyperpycnal flows (Yang *et al.* 2018), but again the animal should then burrow more deeply where the pore water should be more saline. Inflow of hypersaline waters may be considered as well, but the expected reaction of the animal should be the same as in the former case. The proposed answer derives from the fact that spatangoid echinoids burrow just below the redox boundary but need to pump oxygen from above for respiration (Bromley *et al.* 1995), so they have to keep at a certain distance to the boundary. The redox boundary can migrate rapidly up and down, mainly in response to the influx of degradable organic matter (Katsev *et al.* 2006; Wetzel 2010). It is worthy of note that occurrence of *Sursumichnus* igen. nov. in the Satovle-2 section is accompanied by increased abundance of plant detritus (Text-fig. 3). If the redox boundary moved upward for a short period, the echinoid would rest in the shallower zone, where it would not ordinarily feed while burrowing. In particular in turbidites, fining-upward grain size distribution may cause less favourable conditions for burrowing echinoids (e.g., Bromley 1996). After usual conditions re-established while the redox was lowered, the tracemaker withdrew from the resting position and

continued in the usual burrowing depth and produced *Scolicia* (Text-fig. 10). Therefore, *Sursumichnus* igen. nov. could be regarded as a proxy of a short shallowing of the redox boundary. Bromley *et al.* (1995) observed *Echinocardium cordatum* Pennant, 1777 in an aquarium, surviving a four-day-long anoxia in the sediment and water column; the burrowing echinoid moved upward to the sediment surface. *Sursumichnus* igen. nov. records less drastic conditions without retreat of the tracemaker to the surface.

The abundance of *Sursumichnus* igen. nov. on one bedding surface in the Satovle-2 section attains a maximum of 7–10 traces per m². This suggests that the process involved a large number of tracemaker individuals (probably all), including juvenile tracemakers (or different smaller taxa), which produced *S. cf. orbicularis*. Thus, the behavioural shift seems to have been collective and supports the above interpretation.

Sursumichnus orbicularis igen. et isp. nov. occurs in the sections containing several graphoglyptid trace fossils (e.g., *Paleodictyon* isp., *Megagraption* isp., *Protopaleodictyon* isp., *Spirorhapse* isp., *Helminthorhapse* isp.), which are typical components of the *Nereites* ichnofacies, especially the *Paleodictyon* ichnosubfacies (e.g., Uchman and Wetzel 2012). Therefore, *Sursumichnus* igen. nov. can be considered as a component of this ichnofacies and ichnosubfacies. Probably, its occurrence is not limited only to this ichnofacies, as it occurs in the Miocene Upper Marine Molasse in Switzerland (A. Wetzel, personal comm. 2022).

CONCLUSIONS

Sursumichnus orbicularis igen. et isp. nov. from the Palaeogene flysch of the Lesser Caucasus in Georgia is a new ichnogenus and ichnospecies of a resting trace produced by burrowing spatangoid echinoids. It records a stay of the animal after having moved to a shallower position within the sediment. The resting stage was likely caused by temporary shallowing of the redox boundary, which in turn was probably triggered by the influx of degradable organic matter. This trace fossil belongs to the *Nereites* ichnofacies and can serve as proxy of short-term shallowing of the redox boundary.

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