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New rhenopyrgid edrioasteroids (Echinodermata) and their implications for taxonomy, functional morphology, and paleoecology

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Running Header: New rhenopyrgid edrioasteroids and their implications

Abstract.---Rhenopyrgids are rare, turreted edrioasterid edrioasteroids from the lower Paleozoic with a distinctive and apparently conservative morphology. However, new, well preserved rhenopyrgid edrioasteroid material from Canada, along with a review of described taxa, has revealed broader structural diversity in the oral surface and enabled a re-evaluation of rhenopyrgid functional morphology and paleoecology.

The floor plates in *Rhenopyrgus viviani* n. sp., *R. coronaeformis* Rievers and, *R. flos* Klug et al. are well fused to each other and the interradial oral plate and lack obvious sutures, thereby forming a single compound interradial plate. This differs to other rhenopyrgids where sutures are more apparent. Such fused oral surface construction is only otherwise seen in some derived edrioblastoids and in the cyathocystids, suggesting homoplasy.

Our analysis further suggests that the suboral constriction could contract but the flexible pyrgate zone could not. Thus, specimens apparently lacking a sub-oral constriction should not necessarily be placed in separate genera within the Rhenopyrgidae. It also supports rhenopyrgids as epifaunal mud-stickers with only the bulbous, textured, entire holdfasts (coriaceous sacs) anchored within the substrate rather than as burrow dwellers or encrusters.

Rhenopyrgus viviani n. sp. is described from the Telychian (Lower Silurian) Jupiter Formation of Anticosti Island, Québec, Canada and is differentiated by a high degree of morphological variability of pedunculate plates, broader oral plates, and narrower distal ambulacral zones. Specimens lacking or with obscured diagnostic plates from the Ordovician of Montagne Noire, France, and the Ordovician and Silurian of Girvan, Scotland are also described.

Introduction

Rhenopyrgids are an unusual, morphologically distinctive group of edrioasteroids that are rare but both geographically and temporally wide ranging (Sumrall et al., 2013). They are known from all continents except Asia and Antarctica, from lower Ordovician to middle Devonian age rocks. Rhenopyrgids are morphologically highly organised and characterised by a small domed oral surface composed of five short ambulacra with large cover plates, separated by interradial oral plates, an elongated stalk-like pedunculate zone, and a basal coriaceous sac.

The history of taxonomic assignment of rhenopyrgid edrioasteroids is complex but was recently well summarised by Sumrall et al. (2013) and as such, it is not repeated here. However, Sumrall et al (2013) firmly established rhenopyrgids as edrioasterid edrioasteroids that are most closely related to other highly turreted edrioasterids (cyathocystids and edrioblastoids) based on similarities in the structure of the oral surface. The recent description of *Heropyrgus* from the Hereford Lagerstätte by Briggs et al. (2017) has increased the number of genera assigned to the family Rhenopyrgidae Holloway and Jell to two. The key skeletal difference being that *Heropyrgus* apparently lacks cover plates and has floor plates which gape and thereby do not floor the entire ambulacra; a very unusual feature in edrioasteroids (Sumrall, pers. comm. 2018).

Rhenopyrgids have been variously interpreted as living in mud burrows, into which the oral surface may be withdrawn by supposed contraction of the pedunculate zone (Smith and Jell, 1990, Klug et al 2007), or as mudstickers or encrusters with a flexible pedunculate zone (Sumrall et al., 2013). However, there is a lack of direct evidence for any behaviour; none have been found in-situ, either within burrows, affixed to muddy substrates, or encrusting hard or firm substrates.

New material presented here from the Silurian of Canada and various European localities (Ordovician of Girvan, Argyllshire, UK, and Montagne Noire, France) extends the paleogeographical and temporal distribution of this rare fossil group. The new material provides an insight into previously overlooked morphological variability and taphonomic observations which in turn have led to new paleoecological inferences.

Geological setting

New specimens comprising this study were collected from the lower Silurian of Anticosti Island, Québec, Canada, and the Ordovician of Montagne Noire, France and the Girvan district of Scotland. The geological setting of each of these localities will be dealt with in turn, although only the newly erected species from Anticosti Island will be dealt with in detail.

Anticosti Island.---The geology of Anticosti Island comprises Upper Ordovician to Lower Silurian strata (Chatterton and Ludvigsen, 2004) which dips gently to the southeast (See Fig 1.4). The units are dominated by shallow marine carbonate ramp deposits of limestones and shales (Long, 2007). During the deposition of these rocks, the southern margin of Anticosti was most likely exposed to westerly directed tropical cyclones off the Iapetus Ocean, and which deposited frequent tempestites (Wilde, 1991). The rhenopyrgid edrioasteroids were found in two members of the Lower Silurian (Telychian) Jupiter Formation. Almost all specimens of *R. viviani* n. sp. came from the Cybèle Member at collection site 1, but a single specimen came from the Pavillon Member at collection site 2 (See Fig 1.4). Within the published literature, the only other edrioasteroids known from Anticosti Island is *Hemicystites pleiadae* from the Upper Ordovician Vauréal Formation (Sinclair and Bolton, 1965). Unpublished edrioasteroid material has been collected more recently, but none of this included rhenopyrgid edrioasteroids (W. Ausich pers. comm. 2018).

The Cybèle member comprises 32 m of grey, sparsely fossiliferous, lithographic limestone deposited on a broad, south-facing carbonate ramp. Fossils are relatively scarce (M. Martin pers. observ. 2015), but dominated by trilobites and highly endemic crinoids (Ausich and Copper, 2010). The specimens all came from a hard, medium grey, tempestite limestone. Other fossils include current orientated tentaculitids, disarticulated trilobite fragments, and ostracod debris.

The Pavillon Member is composed of 10 m of thin recessive tempestite limestones that are interbedded within grey/green shales. The member is generally highly fossiliferous and rich in brachiopods and trilobites. Other fossils include large numbers of isolated crinoid columnals and several fairly long partially articulated stem fragments, along with disarticulated trilobite remains, bryozoan fragments, and numerous tentaculitids.

The specimens from Anticosti Island are very well preserved in calcite with some evidence of stereom microstructure present (Fig. 2.5, 2.10). Specimens are preserved either lying on the bedding plane and apparently similarly orientated to other tubular fossils (e.g. tentaculites) (e.g. Fig. 2.8), or nearly per-pendicular to the bedding (such as Figs. 2.1, 4). All are preserved in a hard grey micritic limestone. Most specimens display partial crushing, but retain some 3-dimensionality. The oral surface is usually partially collapsed, with disrupted cover plates (Figs 2.1-3, 6, 7, 9), whilst others show disarticulation of the suboral constriction and pedunculate zone (Figs 2.5). The specimens that are preserved perpendicular to bedding surface also suffer either minor crushing or have flattened oral areas (Figs 2.1-4) and loss of the distal pedunculated zone and coriaceous sac. None appear to be in life position or within a burrow. All specimens from the Cybèle member are partially disarticulated and missing parts of the distal pyrgate zone and coriaceous sac. This suggests, in both members, short transportation with preservation occurring after rapid burial.

Ardmillan specimen (Girvan).---The precise locality of the specimen EE 16524 is simply labelled "Ardmillan" and does not have any further specific detail. However, whilst it is different from the well-known Lady Burn Starfish Bed, it is reminiscent of equivalent rock of the Ardmillan Series of the Upper Ordovician (Hirnantian) exposed on the coast to the south of Girvan (in the vicinity of a camp site called 'Ardmillan'). It therefore seems likely to have come from this locality.

The fossil was preserved in an oval concretion comprised of a massive fine, dark grey, muddy sandstone, including numerous larger clasts of detrital calcite. Unusually for Paleozoic echinoderms, EE 16524 is preserved as a 3-dimesional calcite cast (secondary calcite overgrowing primary stereom) composed of a long articulated pyrgate zone missing the adoral structures and basal coriaceous sac. Thus, the imperfect preservation of the specimen and the massive nature of the sediment is again suggestive of short transportation and rapid burial in a mass accumulation.

Montagne Noire specimens.---The Southern Montagne Noire (France) exhibits a rather complete Lower Ordovician succession. Rhenopyrgid material has been collected from the Saint-Chinian, Foulon and Landeyran formations.

The Saint-Chinian Formation (< 500 m thick) consists of monotonous dark-grey clayey siltstones intercalated by fine- to medium-grained sandstones, interpreted as outer-platform deposits (Álvaro et al., 2003). The specimen studied (UCBL-FSL713316) here was collected from the *E. filacovi* Zone (Late Tremadocian) and is preserved as a mould within a grey calcareous concretion in three dimensions. The sediment is a fine siltstone.

The Foulon Formation (80 m thick) corresponds to an alternation of shales, bearing siliceous fossiliferous concretions, and fine-grained sandstones deposited via storm-generated turbidity currents that transported sandy material to offshore settings (Noffke and Nitsch, 1994). The specimen studied here (UCBL-FSL713312) was collected from the transitional beds at the uppermost part of the formation at the top of the *N. arenosus* Zone (middle Floian) and is preserved as a crushed mould within a grey shale (i.e. not within a concretion).

The Landeyran Formation (~300 m thick) is composed of brown, green and grey homogeneous shales bearing siliceous concretions, interpreted as bioclastic storm-deposits in upper offshore environments (Bonin et al., 2007). The specimens studied (UCBL-FSL

713313-5) were all collected from the *A. incisus* Zone and are preserved both as a mould within a grey calcareous concretion in three dimensions (UCBL-FSL 713315) and as a flattened mould within a grey shale (UCBL-FSL 713313-4).

Materials and methods

The specimens new to science which were used in this study come from several locations. These are listed below;

Anticosti Material.---EE 16642 (Holotype), EE 15752-15755 (Paratypes), MPEP 1126.1 (Paratype) all from Rock Pool Ledge, Jupiter River Section, Cybèle Member (Loc. 1 on Fig. 1.3) and EE 15756 (Paratype), from the Pavillon River section, Pavillon Member (Loc. 2 on Fig. 1.3), Anticosti Island, Québec, Canada (Fig. 1). Specimens were found by surface collecting in 06/2011 by T. Vivian, M. Martin, and P. Isotalo.

Ardmillan material.---EE 16254; "Ardmillan", South of Girvan, Girvan District, Ayrshire, Scotland. Method of collection unknown. Found unregistered within the collections of the Natural History Museum London.

Montagne Noire material.---UCBL-FSL 713312; La Croix de Roquebrun, Saint-Nazaire-de-Ladarez, Hérault; UCBL-FSL 713313-4; Pont Supérieur, Saint-Nazaire-de-Ladarez, Hérault; UCBL-FSL713315, Vallée du Landeyran, UCBL-FSL 713316; SW of Donnadieu, Babeau-Bouldoux, Hérault. Specimens were collected by D. Vizcaïno and E. Monceret by surface collection and splitting of concretions.

Methods.---Matrix surrounding the specimens from Anticosti Island was initially removed using an ME-9100 and a Micro Jack #4 air scribe and a Crystal Mark MV-241 Micro air abrasion unit with 40 micron dolomite powder blast media with final uncovering of plates done using a hardened steel needle so as to minimise damage to the surface texture/structure of the plates. Mouldic specimens (from various sites) were cast in latex. All specimens or latex casts were then coated with ammonium chloride and imaged using a Cannon SLR 340 digital camera.

An attempt was made to scan the oral surface of one Anticosti Island specimen (EE 15755) at the CERN light source, Switzerland to understand the internal structure. However, this proved to be unsuccessful owing to insufficient contrast between the matrix and fossil.

Rhenopyrgid morphological terminology follows that of Sumrall et al. (2013). See also Figure 4.1.

Repositories and institutional abbreviations.--- Specimen prefixes are housed in the following institutions:

E or EE are abbreviations of the full prefix NHMUK PI E/EE: Natural History Museum London, UK.

MPEP: Musée de paléontologie et de l'évolution, Québec, Canada.

SNSB-BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Germany.

UCBL-FSL: University Claud Bernard 1, Lyon, France.

USNM: National Museum of Natural History (Smithsonian Institution), Washington DC, USA.

Systematic paleontology

Phylum Echinodermata de Brugiere, 1791 (ex. Klein, 1734)

Class Edrioasteroidea Billings, 1858

Order Edrioasterida Bell, 1976

Suborder Edrioblastoidina Fay, 1962

Family Rhenopyrgidae Holloway and Jell, 1983

Genera included.---*Rhenopyrgus* Dehm, 1961 and *Heropyrgus* Briggs et al., 2017.

Diagnosis (Emended).---Pyrgate edrioasteroids with relatively small oral surfaces bearing five, short, straight rapidly tapering ambulacra; interambulacra formed of single tessellate interradial oral plates and biserial and alternating floor plates that may or may not be fused; cover plates, where present, are biserial and tall proximally; sub oral constriction generally short, composed of circlets of poorly organised imbricate, scale-like plates and periproct, sometimes withdrawn behind collar plates; collar plates large, forming a single imbricate circlet at base of suboral constriction; pyrgate zone long, comprised of 8 rows of highly imbricated scale-like plates arranged in alternating circlets of 4; holdfast formed of coriaceous sac comprised of small unorganized platelets.

Occurrence.---North Africa (Morocco), Europe (Germany, UK, France, Russia, Sweden, ?Spain), North and South America. Tremadocian, Lower Ordovician – Eifelian, Middle Devonian.

Remarks.--- The description of *R. viviani* n. sp. and a detailed reassessment of previously described taxa (see discussion) with well-preserved oral surfaces, has highlighted varying degrees of fusion of the interadial oral plate and the ambulacral floor plates (particularly the externally exposed parts). The ambulacral floor plates of the type species, *Rhenopyrgus coronaeformis* Rievers, 1961, have totally fused to each other and the interradial oral plate (Fig. 3.9, 10), whilst plate sutures are visible in *Rhenopyrgus grayae* Bather (Fig 3.1). This highlights greater structural diversity than was previously thought, which, as well as broadening the familial diagnosis, also enables a re-evaluation of the relationships with other edrioasterids that have a similar oral arrangement (see below).

The discovery of a well preserved anal pyramid in the holotype of *R. viviani* sp. nov. confirms the suggestion of Sumrall et al., (2013) and Holloway and Jell (1983) that the periproct is located within the suboral constriction, adjacent to an oral plate in the CD interray. This location is similar to that seen in other edrioasterids (Bell, 1976) and *Heropyrgus* (Briggs et al., 2017).

Briggs et al. (2017) recently erected *Heropyrgus* within the Rhenopyrgidae as it shared many key characteristics of skeletal organisation and differed only by lacking cover plates and, that the floor plates gaped and did not completely floor the ambulacra, although these variations were not included in an emended diagnosis. However, the lack of the cover plates and the unusual arrangement of the ambulacral floor is very curious, particularly as the ridged adambulacra margin of the oral and floor plates look very similar to those of other rhenopyrgid genera that clearly bear cover plates (particularly *R. viviani* sp. nov. (Fig. 2.2). As such, taphonomic loss and/or disruption should be considered a possibility for cover plates lacking in specimens assigned to *Heropyrgus* and potentially the ambulacral gape. That said, in lieu of further evidence, this genus must currently be maintained and its variations included in the family diagnosis.

Following Holloway and Jell (1983), Sumrall et al. (2013) placed rhenopyrgid species into their own family; however, they questioned the validity of classifying specimens based solely on characters of the pyrgate and pedunculate zones or where they lacked well preserved oral areas. As such, Sumrall et al. (2013) removed all such examples from the genus *Rhenopyrgus*, but retained them within the Rhenopyrgidae Holloway and Jell (1983) on account of the pyrgate zone being formed of 8 rows of plates. We follow this approach here.

Sumrall et al. (2013) also suggested the removal of generic assignation of rhenopyrgid taxa that lacked a suboral constriction. Thereby suggesting *Rhenopyrgus grayae* Bather (1915) and possibly *R. flos* Klug et al. (2008) should be placed in a separate genus. However, we believe that the lack of a sub-oral constriction is taphonomic in rhenopyrgids (see discussion section). As such, we assign both these species to various respective genera which also include taxa with clearly preserved suboral constrictions.

The higher taxonomic relationship of rhenopyrgids were reviewed by Sumrall et al. (2013) who, in agreement with previous workers, suggested that rhenopyrgids are edrioasterids united with edrioblastoids and cyathocystoids by the reduced number of interambulacral plates, the pseudo fivefold symmetry of the ambulacral system, and the turreted thecal shape. These groups differ from one another primarily in the form of the pedunculate zone—organized flexible stalk in rhenopyrgids, fused cup in cyathocystids, and an elongate, rigid, multiplated stem in edrioblastoids. However, Sumrall et al. (2013) left the specific relationships between these families open. Sprinkle and Sumrall (2015) drew closer affinities between cyathocystids and derived edrioasterids as both shared a similar oral surface construction, formed by fusion of the floor plates to each other and the interadial oral plate. However, these comparisons were made on the assumption that all rhenopyrgid taxa did not possess this feature, which we here demonstrate is not the case. We cannot really add anything further to refine these relationships other than highlight that all three turreted edrioasterid families display similar ambulacral structures in various constituent species. As suggested by Sprinkle and Sumrall (2015) for cyathocystids and derived edrioblastoids, this suggests some form of homoplasy/convergence which was particularly suitable for turreted edrioasterid ecology.

Genus *Rhenopyrgus* Dehm, 1961

Type species.---*Pyrgocystis (Rhenopyrgus) coronaeformis* Rievers, 1961; Hunsrück Slate, Lower Devonian, (Emsian) of Germany.

Species included.---*Rhenopyrgus coronaeformis* Rievers, 1961; *R. flos* Klug, Kröger, Korn, Rücklin, Schemm-Gregory, de Baets, and Mapes, 2008; *R. viviani* n. sp.; *R.* sp. indet.1 (formerly *Pyrgocystis procera* (Aurivillius) Bather, 1915); R. sp. indet. 2, *R.* sp. indet. 3, *Rhenopyrgus* sp. indet. 4.; *R. grayae* (Bather, 1915); *R. whitei* Holloway and Jell, 1983; and *R. piojoensis* Sumrall, Heredia, Rodríguez, and Mestre, 2013.

Emended diagnosis.---Rhenopyrgids with fused or unfused ambulacral floor and interradial oral plates; suboral constriction, formed of a zone of highly imbricate elongate plates formed between the oral surface and suboral collar, may or may not be exposed. Cover plates present.

Occurrence.---Lower Ordovician (Tremadocian) to Lower Devonian (Emsian); from France (Lower Ordovician, Upper Tremadocian and Floian), UK (Katian, Upper Ordovician and Middle Llandovery, Lower Silurian), Canada (Ruddanian, Lower Silurian), Argentina (L. Ludlow, Upper Silurian), Australia (L. Devonian), Morocco (Emsian, Lower Devonian), and Germany (Emsian, Lower Devonian).

Remarks.--- There is significant variation in the fusion of the interradial oral plates with the ambulacral floor plates in different species throughout the range of *Rhenopyrgus*. Some (e.g. *Rhenopyrgus coronaeformis*, *R. flos*, and *R. viviani*) display complete fusion, giving the appearance of only a single D-shaped interradial plate with a broad curved ambital margin. It is tempting to using this character to subdivide the genus further, however there are few other characters which either unify or differentiate these taxa from those with unfused (or less completely fused) oral surfaces. As such, until detailed cladistic analyses are employed we with-hold from formerly erecting a new genus for these taxa with unfused floor plates (as the type species *R. coronaeformis* clearly displays fused interaidal and ambulacral floor plate elements, see Fig. 3. 9-10).

The fusion of the interradial and floor plate systems however means that isolated D-shaped oral plates, with either smooth or notched margins, that are found in close association with articulated sections of pyrgate zone comprised of 8 rows of plates, which may or may not also lack clearly defined collar and suboral constriction plates (as these plates are determined to be moveable and therefore could have contracted within the pyrgate zone and be obscured e.g. Fig 2.3-4), can now be used to imply classification to *Rhenopyrgus*. Owing to the presence of such associations, *Rhenopyrgus* sp. indet. 1 (formerly *Pyrgocystis procera* [Aurivillius] Bather, 1915) from the Lower Silurian Newlands Beds of Newlands, Girvan, Ayrshire, Scotland (Fig. 3.3-4), *Rhenopyrgus* sp. indet. 2 from the Ordovician of Ardmillan, Girvan, Ayshire, Scotland (see below), *Rhenopyrgus* sp. indet. 3 from the Montagne Noire, France (see below), *R. flos* (Klug et al., 2008) from the Devonian of Morocco, and *Rhenopyrgus* sp. indet. 4 (as illustrated by Grigo 2000) can all be assigned to this genus.

Rhenopyrgus viviani new species

Figures 2 and 4.

Holotype.---EE 16642, Paratypes EE 15752-15756 and MPEP 1126.1. Cybèle Member, Jupiter Formation, Telychian, Upper Llandovery, Lower Silurian from Rock Pool Ledge, Jupiter River, Anticosti Island, Québec, Canada,

Diagnosis.---*Rhenopyrgus* with interambulacra composed of a single broad, relatively low D-shaped compound interadial plate with gently curving adambulacral margin. Distal cover plates distinctly square. Adoral constriction composed of 3-5 circlets. Plates of the pedunculate zone vary in morphology of exposed aboral margin, being curved adorally but becoming distinctly rhombic (angular) aborally.

Occurrence.---Cybèle Member to Pavillon Member, Jupiter Formation, Telychian, Upper Llandovery, Lower Silurian, Anticosti Island, Québec, Canada (see above for details).

Description.--- Oral surface domed with straight ambulacra, fairly evenly spaced but with a vestige of 2-1-2 ambulacral arrangement (Sprinkle 1973) apparent (Fig. 2.2-4). External oral surface composed of biserial, alternating, tesselated cover plates with zig-zag suture and tessellated, D-shaped, compound interradial plates (formed of fused interradial oral plate and ambulacral floor plates) lacking in obvious sutures (in un-weathered specimens) and, with curved adambulacral margins. Cover plates number 12-16 per interradial oral plate, 6-8 in each ambulacrum (Figs. 2.2-7). Proximal cover plates long thin rectangles with triangular or T-shaped cross sections (Figs. 2.7, 9), but grade distally into shorter, wider, more equi-dimensional (square) plates (Figs. 2.4,5, 9). All cover plates articulate in grooves formed by ridges along the margin of the compound interradial plates (Figs. 2.2-3, 4.2). Below cover plate articulation areas, the ridges anastomose or become off-set, forming a distinct set of ridges. Ambulacral floor not adequately seen in any specimen, but proximally appears to be a formed by the ridged shallow slope of the adambulacral margin of the compound interradial oral plate. Distally, floor plates appear to have a similar morphology (Figs. 2.2-3, 4.2). Aboral margin of interradial oral plates straight and abut along oral surface ambitus with imbricate plates of suboral constriction zone.

Suboral constriction composed of at least 3-5 circlets of less regularly aligned, highly imbricating, wedge-shaped plates which increase in size distally, but which are comparatively small compared to those of collar and pyrgate zone (Fig. 2.5-7, 9). Distally these circlets are bordered by a circlet of larger, rectangular imbricated plates which form collar (Fig. 2.5-7, 9). Periproct (Fig. 2.7, 4.1) located in CD interray adjacent to oral plate margin, composed of a single circlet of short imbricated rectangular plates. Gonopore and hydropore unknown.

Pyrgate zone highly organised into alternating circlets of four, highly proximally imbricating plates. Plates form alternate circlets aligned into straight longitudinal columns of at least 52 (in the only known specimen with a complete pedunculate zone) such that eight peduncular ridges are present. Four plates from each circlet meet beneath the more distal circlet to form a ring with a fairly large lumen, Plates are squamose proximally with broadly rounded outline becoming distinctly more angular distally in the holotype and smaller specimens (Fig.2.6, 9) but variation less apparent in large individuals (e.g. in EE 15756). Coriaceous sac bulbous at base, approximately a quarter of length of pedunculate zone and slightly wider. It is formed of numerous randomly organised platelets (Fig.2.10).

Etymology.---Named for the initial discoverer Mr. Travis Vivian.

Materials.---EE 16642 (Holotype), EE 15752-15756 (Paratypes), MPEP 1126.1 (Paratype), MPEP1143.1.

Remarks.---This taxa is differentiated from most other species of *Rhenopygus* by the fusion of interradial oral plates and the external portions of the floor plates, thereby giving the impression of cover plates being supported by a single interradial oral ossicle. Of the other *Rhenopygus* species which also display this fusion, the oral surface of *R. viviani* is not so highly domed, the oral plates are lower, wider and more rounded adorally, with narrower distal ambulacra. The pedunculate zone is also much more highly variable along the length than in other taxa.

The low ridges or walls between floor plates and along the ambulacral margin of the oral plates (producing a series of grooves) are remarkably similar to the higher ridges seen in *Heropyrgus*, were they also accommodated the tube feet (Briggs et al., 2017). Therefore, it seems reasonable to assume these ridges served a similar function in *R. viviani* and/or are muscle/ligament attachment scars for closing the cover plates.

The less formal arrangement of the plates of the suboral constriction, their high degree of imbrication coupled with a rather inconsistent exposure of plates, and number of circlets present in various individuals from the same locality suggest they were capable of vertical extension and contraction. This agrees with observations of *B. piojoensis* (Sumrall et al., 2013).

Despite the oral surface being crushed in specimen EE 15756 from the Pavillon Member, it differs from specimens of the Cybèle Member only in there being a smaller amount of change in the morphology of the pedunculate zone plates, although there is still some discernible change. Subtle changes in pedunculate plate morphology were also noted between larger and smaller individuals by Sumrall et al. (2013) in a population of 84 *R. piojoensis* but this variation was not as obvious as in *R. viviani* n. sp.

Rhenopyrgus grayae (Bather, 1915)

1915 *Pyrgocystis grayae* Bather, p. 58, pl. 3, figs. 1-2.

1983 *Rhenopyrgus grayae* Holloway and Jell, p. 1002, 1004

1985 *Rhenopyrgus grayae* Smith, p. 732, Text-fig.11

2013 *Pyrgocystis grayae* Sumrall et al., Fig. 1

2013 *Rhenopyrgus grayae* Sumrall et al., p.773

Holotype.---E 23470. Upper Ordovician, Katian, Ardmillan Series, Drummuck Group, South Threave Formation, Farden Member, Lady Burn Starfish Bed, part of the Craighead inlier.

Diagnosis (Emended).---*Rhenopyrgus* with highly domed oral surface. Oral plates narrow and high with acutely curved adambulacral margin. Ambulacral zone prominent with long proximal cover plates and wide distal ambulacral zone.

Occurrence.---Known only from the Upper Ordovician, Katian, Ardmillan Series, Drummuck Group, South Threave Formation, Farden Member, Lady Burn Starfish Bed.

Description.---*Rhenopyrgus* with well-preserved oral surface comprising of long proximal and distal cover plates arranged in fairly symmetrical pattern but with a vestige of 2-1-2 pattern discernible, oral plates fairly rectangular with a narrow ambital margin and acutely curved adoral margin. 3 discernable floor plates form distal part of ambulacra and together give the interradial oral area a deltoid-shape. Only part of a single plate of the sub-oral constriction is visible between proximal margins of collar plates. Collar plates large and rectangular with curved proximal margins. Two ridges on distal external surface of collar plates run down behind proximal plates of pyrgate zone. Pyrgate zone distinctly tapering and comprised of squamate imbricate plates with curved proximal margins arranged in circlets of 4, forming 8 rows; 58 circlets in only complete specimen (holotype). Coriaceous sac comprised of a granular membrane with bulbous base.

Material studied.---E 29570, E 23674.

Remarks.---This taxa was erected by Bather (1915) with the diagnosis focused primarily on the morphology of the pyrgate zone. Sumrall et al. (2013) questioned the validity of erecting taxa based solely on pedunculate zone morphology, and thus we here emend the diagnosis to include characters of the oral surface.

Whilst Sumrall et al. (2013) regarded this taxa as a member of the Rhenopyrgidae, the apparent lack of a suboral constriction led them to suggest that it should be placed into a new, as yet, undescribed genus. However, we believe that the apparent lack of a suboral constriction is a feature of taphonomy and that the sub-oral constriction has been withdrawn behind the collar plates. As this specimen is preserved as a mould, the plates of the sub oral constriction are no longer clearly visible. However, a clue to its presence can be seen in Fig. 3.1 (highlighted by a white arrow), where the distal portion of a plate is just visible between two collar plates, exactly where one would expect to see such a plate if the sub-oral constriction zone were withdrawn. As such, we feel that there is no need to erect a new genus specifically for this and other Rhenopyrgid taxa apparently also lacking a sub-oral constriction.

R. grayae displays suture lines between the plates of the oral surface, particularly between the interradial oral plates and the external portions of floor plates, distinguishing it from *R. viviani*, *R. coronaeformis*, and *R. flos*. Of the *Rhenopyrgus* taxa which also display suture lines between the oral and floor plates *R. grayae* can be distinguished by its high, narrow, oral plates with a relatively gentle apical curve and its broad distal ambulacra and cover plates. Both *R. whitei* and *R. piojoensis* have more acute apical angles, with the former having distal ambulacra that narrow more abruptly, whilst the latter has narrower distal ambulacral and cover plates.

Rhenopyrgus sp. indet. 1

1915 *Pyrgocystis procera* (Aurivillius) Bather, p. 59.

2013 *Rhenopyrgus*? *procera* Sumrall et al., Fig.1 C, p.764.

Occurrence.---Known only from the Lower Silurian, Middle Llandovery, Saugh Hill Group, Newlands Subgroup, Newlands Farm Formation, Newlands Beds, but may extend into the Ardmillan group of the Upper Ordovician (see remarks).

Description.---Only known from one relatively complete specimen, E 62753 (Fig. 3.3-4), others comprise only sections of pyrgate zone. This specimen has standard *Rhenopyrgus* construction, with turreted theca divided proximally to distally into an oral surface, collar, pedunculate zone, and coriaceous sac. Suboral constriction not apparent, but this is assumed to be a feature of taphonomy and that it is obscured by collar plates.

Oral surface only known from one crushed specimen (E 62753) displaying a single large, D-shaped, compound, interradial plate pressed down into top of pyrgate zone (Fig. 3.4). Cover plating and ambulacra unknown. Suboral constriction plating unknown. Collar plates indistinct but appear wider than other pedunculate plates and form a circlet at the top of the peduncle. Pyrgate zone, slightly curved and composed of approximately 48 circlets in longest specimen (E 62753). Circlets comprised of fairly narrow squamate plates, with curved proximal margin although many are broken giving a more angular look (Fig. 3.3).

Circlets are arranged at highly inclined angle. Coriaceous sac comprised of numerous small platelets.

Materials.---E 62753, E 62751, E 62752.

Remarks.---The material from the Newlands beds was originally assigned to *Pyrgocystis procera* (Aurivillius) by Bather (1915) owing to similarities in the morphology of the pedunculate zone. However, Bather (1915) expressed concern about the validity of erecting a species solely on the morphology of the pedunculate zone. Sumrall et al. (2013) suspected that this species was actually a Rhenopyrgid on the basis of the pyrgate zone plating and coriaceous sac, but did not formerly transfer this species to the genus, owing to uncertainty surrounding the nature of the oral surface and suboral contraction.

On reanalysis of the material, we interpret a large D-shaped plate within the top of the pyrgate zone in specimen E 62753 as a compound interradial plate (Fig. 3.3) seen in other species of Rhenopyrgus with fused floor and interradial oral plates. The position and morphology of this D-shaped plate are similar to the disarticulated oral surfaces of *R. flos* (see Klug et al., 2008 Plate 16.4 and Text-fig. 25), although they lack the prominent ridges on the margins. Specimen E 62753 also displays many other features compatible with *Rhenopyrgus* including an enlarged circlet of proximal pedunculate plates, which we interpret as collar plates, whilst the lack of a discernible suboral contraction may be a feature of taphonomy (i.e. it was withdrawn behind the collar plates - see comments in Functional Morphology section). Thus, we tentatively assign these specimens to the genus *Rhenopyrgus*. However, we agree with Sumrall et al. (2013) (and Bather, 1915 in part) that species should not be solely based on morphology of the pedunculate zone. As the type material of Aurivillius (1892) consists only of pedunculate plates, we consider *Pyrgocystis procera* a *nomen dubium*, and owing to the imperfect preservation precluding adequate comparison with other *Rhenopyrgus* species we assign this material to *Rhenopyrgus* sp. indet. until better material is found.

Whilst the incomplete preservation of this occurrence precludes detailed comparison of all features with other named *Rhenopyrgus* species, useful comparisons can still be made. The pyrgate zone most closely resembles in both size and morphology those of *Rhenopyrgus* indet. 2, from the nearby Girvan site of "Ardmillan", but which is probably from slightly older strata (see below). As such, it is described separately but may in fact belong to the same, albeit indeterminable, taxon. The apparent fused nature of the interradial oral plating discounts affinities to *R. grayae* (Bather) comb. nov., which is also found from slightly older rocks nearby or *Heropygus* Briggs et al., (2017). Otherwise it is stratigraphically and morphologically most similar to *R. viviani* n. sp. but has slightly higher and narrower oral plates.

Rhenopyrgus sp. indet. 2

Occurrence.---"Ardmillan", [?Girvan], Scotland, UK, Ardmillan Series. Part of the Craighead inlier, Katian, Upper Ordovician.

Description.---Single specimen, displaying long portion (31mm) of pyrgate zone comprised of at least 38 alternating circlets in 8 columns (Fig. 3.5). Pyrgate zone plates large, steeply inclined, widely spaced and highly imbricating. Shape of plate margins unknown because all are damaged. Oral surface, suboral contraction, collar plates and corriaceous sac are either not preserved or exposed. Oral plating known only from a single disarticulated D-shaped ossicle with a ridged margin.

Materials.---EE 16254.

Remarks.---Only a single, poorly located specimen is known, however a curious disarticulated D-shaped ossicle, found in close association to the articulated portion pyrgate zone (Fig. 3.5), closely resembles a fused interradial plate of *Rhenopyrgus*. On this, rather tentative basis, we assign this specimen to *Rhenopyrgus* sp. indet. Whilst the shape of the interradial plate and the size and morphology of the pedunculate zone distinguishes it from the stratigraphically similar *B. grayae*, it instead resembles that of *R.* sp. indet. 1, formerly described as *Pyrgocystis procera* Bather, 1915 (see above). Owing to the incompleteness of the material from both localities and the apparent stratigraphical differences, we describe it separately and await the discovery of better preserved material for further comparison.

Rhenopyrgus sp. indet. 3

1999 ?*Pyrgocystis* sp. (Bather, 1915) Vizcaïno and Lefebvre, p. 356.

2001 ?*Pyrgocystis* sp. (Bather, 1915) Vizcaïno et al., p. 218.

2013 Rhenopyrgidae Sumrall et al., p.773

Occurrence.---(UCBL-FSL 713316) SW of Donnadieu, Babeau-Bouldoux, Hérault, France, *E. filacovi* Zone, Saint-Chinian Formation, late Tremadocian, Lower Ordovician. (UCBL-FSL 713312) la Croix de Roquebrun, Saint-Nazaire-de-Ladarez, Hérault, France, *N. arenosus* Zone, Foulon Formation, middle Floian, Lower Ordovician; (UCBL-FSL 713313-5) Pont supérieur, Saint-Nazaire-de-Ladarez, Hérault, France, *A. incisus* Zone, Landeyran Formation, late Floian, Lower Ordovician;

Description.---Known from several specimens with well-preserved portions of pyrgate zone and coriaceous sac but disrupted or obscured portions of oral surface and sub oral constriction. Oral surface in UCBL-FSL 713312 is very confused and it is difficult to discern any structures with confidence, precise arrangement or morphology of cover plates difficult to determine; however, suspected interradial oral plates appear D-shaped (see black arrow on Fig. 3.7). Suboral constriction in UCBL-FSL 713312 and UCBL-FSL 713316 obscured by a prominent circlet of rectangular collar plates, with curved proximal edges (white arrows in Fig. 3.7, 8). Pyrgate zone long, either distinctly tapering or parallel sided; formed of small, low, squamate, imbriacated plates arranged in 8 rows of 4 alternating circlets, all with uniform curved proximal margins (64 circlets in only complete specimen); broader proximally, transitioning abruptly into coriaceous sac composed of small, randomly arranged, granular platelets distally.

Materials.--- UCBL-FSL 713312-6. Specimens are found both flattened in shale and as 3 dimensional moulds in sideritic concretions.

Remarks.---The specimens from Montagne Noire are the same as those referred to by Vizcaïno and Lefebvre, 1999 and Vizcaïno et al., 2001 as '?*Pyrgocystis* Bather (1915)' but which are actually rhenopyrgids (Sumrall et al., 2013). The D-shape of the suspected interradial oral plates in UCBL-FSL 713312 and similarities in the pygate zone means we tentatively suggest these specimens belong to the genus *Rhenopyrgus*. They are here described together as there is little to justify their division into different taxa apart from minor variations in stratigraphy. However, pyrgate zone morphology is not a satisfactory taxonomic character, and thus this grouping is provisional.

Despite UCBL-FSL 713312 being relatively complete, the oral surface is highly disrupted making further detailed taxonomically relevant observations impossible. Whilst several specimens display a distinctly tapering pyrgate zone, such morphology is observed in several other rhenopyrgid taxa, particularly *R. grayae*, and cannot be used to differentiate it as a new species. Thus, as key taxonomic characters to differentiate this taxa from other rhenopyrgid species are not satisfactorily exposed, it seems prudent to wait for better preserved material to become available before erecting a new species. They are recorded here for completeness and are perhaps notable as being the oldest *Rhenopyrgus*/rhenopyrgid yet identified.

Discussion

The morphology of rhenopyrgids has long been thought to be fairly conservative (Sprinkle and Sumrall, 2015). However, the description of new taxa here and the re-evaluation of previously described material have resulted in the identification of wider morphological variation. This has implications for supra-familial relationships with other edrioasterids and function.

Variation in the oral surface and its implications.---Specimens of *Rhenopyrgus viviani* n. sp. have some of the better preserved external oral surfaces of any rhenopyrgid taxa yet described. This, along with the partial disarticulation of several *R. viviani* specimens, the re-examination of previously described material, particularly the re-imaging of the genotypic specimen *Rhenopyrgus coronaeformis* Rievers (Fig. 3.9-11), and the description of *Heropyrgus disterminus* by Briggs et al. (2017) has enabled novel observations, particularly of the organisation of the oral surface and the position of the periproct.

Externally, there are no apparent sutures visible between the interradial oral plate and floor plates in *R. viviani* (Figs. 2.2-9), *R. coronaeformis* (Fig. 3.10 black arrow), and *R. flos* (Klug et al., 2008 Text-fig. 25 and Plate 16 8). Instead, the interradial area on the oral surface appears to be occupied by a single deltoid or D-shaped plate, which supports cover plates articulating in grooves along the entire length of the adambulacral margin (Fig. 2.2). However, in *R. grayae*, *R. piojoensis* and, *H. disterminus* the suture lines are more visible and distally the floor plates can be distinguished and seen to support individual cover plates. An arrangement and geometry identical to that seen in *Edrioaster* (Bell 1976) and other primitive edrioblastoids (Smith and Jell 1990). Thus, it appears that in *R. viviani* and *R. coronaeformis* the interradial oral plate and the floor plates have become completely fused into a single compound element as seen in derived edrioblastoids (such as *Lampteroblastus* Guensburg and Sprinkle 1994 and *Porosublastus* Sprinkle and Sumrall 2015) and cyathocystids (Sprinkle and Sumrall 2015). Fusion of these elements into a single compound plate, rather than loss of floor plates, is supported by the presence of faint suture lines in the distal radial parts of the interradial oral plate in a weathered specimen of *R. viviani* (MPEP1143.1) and evidenced by sweeping extinction of this element in thin sections of cyathocystids (Sumrall, C. pers. comm. 2018).

In specimen MPEP1126.1 of *R. viviani* n. sp. the disturbed oral surface suggests the ambulacra are floored by an inclined projection of the proximal margin of this compound plate margin. A row of oval depressions occur in areas just internally of the cover plate grooves, where the walls which maintain the cover plates in position appear to anastomose or become offset (Fig. 2.2 black arrows). Again, this is similar to what is observed in derived edrioblastoids (such as *Lampteroblastus* Guensburg and Sprinkle, 1994) and cyathocystids (Guensburg and Sprinkle, 1994 fig. 17 D; Sprinkle and Sumrall 2015). Previously, such an oral arrangement was suggested to only occur in cyathocystids and independently in derived edrioblastoids, although this was used to imply a closer relationship to each other than either to rhenopyrgids by Sprinkle and Sumrall (2015). Thus, the occurrence of this feature in some rhenopyrgids suggests convergence (homoplasy). This may have been part of a suit of adaptations to form an oral surface better able to resist compressional forces (further discussed below).

The ambulacral structure of *Heropyrgus* (Briggs et al., 2017) differs only in that it lacks cover plates and that, internally, the floor plates do not meet medially and thus the ambulacral floor was not mineralised and the remaining elements gapped. The water vascular system in *Heropyrgus* therefore seems to have been suspended within unmineralised tissue and subsequently there are no skeletal pores. What is similar between *Heropyrgus* and *Rhenopyrgus* (as well as cyathocystids and derived edrioblastoids) is the ridged nature of both the adambulacral margin of the oral plates and floor plates. It is curious that *Heropyrgus* should retain ridged adambulacral oral plate margins given the apparent lack of cover plates. However, these ridges may have been retained as they may have supported and shielded the tube feet when they were extended. However, it is unknown if the ambulacra gape internally in *Rhenopyrgus*. We think that this is unlikely, as there is no evidence to suggest that it did and that other turreted edrioasterids display conventionally organised ambulacra floor plates (Mintz, 1970; Guensburg and Sprinkle, 1994; Sprinkle and Sumrall, 2015), and is highly unusual in edrioasteroids.

In addition to the comments by Sprinkle and Sumrall (2015) regarding comparison of the oral surface construction between cyathocystids, edrioblastoids, and rhenopyrgids, a distinct difference between the former two families and rhenopyrgids is the presence of large “primary peristomal cover plates” (*sensuo* Kammer et al., 2013) that support adjacent cover plates, as seen in *Cyathocystis* (Bell, 1982) and *Astrocystites* (see Kammer et al., 2013 and also Fig. 2 B of Zhu et al., 2014, Fig. 34 of Smith and Jell, 1990 and Fig 174. 1 of Fay, 1967 for this feature in other basal edrioblastoids). This feature is however lost in derived edrioblastoids (e.g. *Lampteroblastus* Guensburg and Sprinkle, 1994) and is yet to be observed in any rhenopyrgid taxa. This may suggest a selective pressure for this feature to be lost independently in two distinct lineages, rather than reflect any phylogenetic relationships, but this needs to be tested further.

The phylogenetic trichotomy of rhenopyrgids, cyathocystids and edrioblastoids (Sumrall et al. 2013 fig. 2) cannot be resolved without further observations. Some of the similarities observed in the three groups (cover plates articulating directly on the oral plates and floor plates fused into a compound plate) may have appeared independently in each lineage. It does however challenge the suggestion of Sprinkle and Sumrall (2015) that cyathocystids and derived edrioblastoids are more closely related as they share a similar ambulacral structure, as this is now observed in rhenopyrgids also.

The holotype of *R. viviani* sp. nov. displays a well preserved short periproct composed of thin elongate rod-like plates surrounded by several small square shaped plates (Fig. 2.7). It is significant as it confirms the tentative observations of Sumrall et al. (2013) and Briggs et al. (2017) that the periproct is located in the suboral constriction adjacent to the interradial oral plate in rhenopyrgids. This construction looks very similar to that seen in *Cyathocystis americanus* Bassler, 1936 (USNM 144878) and, to a lesser extent, that seen in *Edrioaster bigsbyi* Billings, 1857 and *Edriophus lavis* Bather (1914). In edrioasteroids, the periproct is located in the C-D interray. This is significant as it suggests the location of other structures, particularly the hydropore, which is usually located either within the C-D interradial oral plate or along its distal margin (Bell, 1976). In *Cyathotheca*, the hydropore has been tentatively located within the interradial oral ("deltoid") plate, although this is only identified in one specimen (Bockelie and Paul, 1983). Unfortunately, the periproct obscures much of the central and distal part of the C-D interradial oral plate and its margin in the *R. viviani* holotype (Fig 2.7). Furthermore, this feature was also not recorded by Briggs et al., (2017) during their study of *Heropyrgus*. Thus, the location of the hydropore remains obscure in rhenopyrgids.

Rhenopyrgid functional morphology.---Specimens of rhenopyrgids show great variability in the nature of preservation and the manner of skeletal deformation and disarticulation. This has led to a variety of interpretations of functional morphology. The oral surface has been interpreted as relatively fragile compared to the pyrgate zone (Sumrall et al., 2013), with the cover plates either opening individually (Sumrall et al., 2013) or simultaneously along the entirety length of the ambulacra as they are interlinked (Bartels et al., 1998). The suboral constriction and collar has been identified as flexible (Smith, 1985, Sumrall et al., 2013) whilst the whole pedunculate zone has been suggested to have been contractile so as to withdraw the animal into a burrow by Klug et al. (2008) or that the whole pedunculate zone remained in a burrow with only the oral surface exposed (Smith and Jell, 1990). The coriaceous sac has been long identified as an attachment structure (Bather, 1915, Rievers, 1961); however, it has been variously identified as only attaching at the very base to a hard/firm substrate or inserted into mud (Bather, 1915, Sumrall et al., 2013) or as being inserted into mud, along with some or all of the pyrgate zone (Holloway and Jell, 1983, Klug et al., 2008). The new material described here enables a review of these previous suggestions and new observations to be made.

Functional morphology of the oral surface.---The oral surface of rhenopyrgids is frequently disarticulated or missing (Figs. 3.3-8), with disarticulation of the cover plates taking the form of individuals out of place (Fig. 2.2), the entire ambulacra opened like a fan (Figs. 2.7, 9 and 3.9), or cover plates absent with just disarticulated oral plates remaining

(Fig. 3.4 and Klug et al., 2008). This has led to the notion that the oral surface was not such a robust structure when compared to the more commonly articulated plates of the pedunculated zone (Sumrall et al., 2013). Whilst true, there are however many apparent adaptations to strengthen the oral surface. Primarily, the reduced number of plates (and thereby sutures/potential lines of failure), their tessellated nature, and the varying degrees of fusion of the floor plates to the oral plates which must also have strengthened this area by reducing the number of planes of weakness.

The cover plates also display many examples of strengthening. They are generally robust, tessellate without gaps or pores, have an off-set triangular cross section with a flat external surface, and a proximally positioned internal keel (e.g. Fig. 2.7), which presumably acted both to strengthen the plate and provide a wider attachment site for ligaments and muscles to close them. Furthermore, the bases of the cover plates in *Rhenopyrgus* are held in place by grooves in the adambularcral marginal wall of the interradial oral plates (e.g. Figs. 2.2 and 3.9). In *R. coronaeformis* (Fig. 3.9-10) the cover plates display a complex system of teeth and sockets which enabled the cover plates to interlock together. This interlocking seems very effective as the partially disarticulated cover plates are frequently preserved in a manner resembling a fan and have opened along the ambulacral midline (e.g. Figs. 3.9-10 and Bartels et al., 1998 fig. 174). Similar fan like arrangements are also suggested in several *R. viviani* n. sp. specimens (Figs. 2.2, 3, 6-7 and 9) as well as in cyathocystids (Bockelie and Paul, 1983). The fan-like opening of the ambulacra of *R. coronaeformis* were suggested by Bartels et al. (1998) as evidence that the cover plates opened simultaneously along the midline of the ambulacra via articulation along the aboral margin of the oral plates, in a manner identical to that proposed by Bockelie and Paul (1983) for cyathocystids. However, we prefer to interpret the cover plates being able to open individually, as well as simultaneously, by articulation along the adambulacral margin of the oral plates owing to the cross sectional morphology of the cover plates and that each was inserted individually within groves on oral plate margins in *Rhenopyrgus*. What is apparent in these taxa though is that the cover plates had several adaptations to strengthen the oral surface.

Thus, the plate adaptations of the oral surface seen in *Rhenopyrgus*, cyathocystids, and derived edrioblastoids might be understood as derived features to strengthen the oral surface from a more plesiomorphic typical *Edrioaster*-type arrangement of unfused floor plates bearing the cover plates. The oral surface might have disarticulated more rapidly than other parts of the skeleton (particularly the pyrgate zone) because the elements it is comprised of were, in part, moveable in life or were supported by plates of the sub-oral constrictions which was also moveable (see below).

Functional morphology of the pedunculate zone (suboral constriction, pyrgate zone and coriaceous sac).---The suboral constriction is composed of several circlets of highly imbricated plates, which vary in size and shape. This zone has frequently been invoked as being flexible (Klug et al., 2008, Sumrall et al., 2013) and/or able to contract along with the pyrgate zone (Klug et al., 2008). We agree that the suboral constriction zone was both flexible and able to contract; however, we are sceptical of the ability of the pyrgate zone to contract (see below).

A single slab containing 84 specimens of *R. piojoensis* was described by Sumrall et al. (2013), where it was noted that several individuals lacked the plates of the suboral constriction and interpreted them as being obscured by the collar plates (see Sumrall et al., 2013 figs. 6 D and G), whilst others had greatly extended zones. This is precisely what would be expected if the suboral constriction was contractile. Indeed variation in the extension of the suboral constriction is seen in several other taxa (e.g. *R. viviani* n. sp. Figs. 2.5, 6-7), although not to the extent as has been observed in *B. piojoensis*. Furthermore, in *R. grayae*, whist the majority of the sub-oral constriction is absent a small proximal part of a plate is visible between the margins of two collar plates, distal to the oral surface (see Fig. 3.1 white arrow). This seems likely to be the proximal most part of a proximal plate of the sub oral constriction and appears precisely where we would predict it would be if the zone was preserved contracted. If we assume that this zone is contractile in all rhenopyrgids, then it is of taxonomic significance, particularly for the holotype of *R. grayae* (See Fig. 3.1-2), but also *R. flos* Klug et al. (2008 plate 16 figs. 1-14), where an apparent lack of a suboral constriction was suggested by Sumrall et al. (2013) to be grounds to place such occurrences in new genera. However, if this feature is just a taphonomic artefact, it is not a reliable taxonomic feature and should not be used. Accordingly, it also enables the inclusion of material which otherwise display all other rhenopyrgid morphological characters to named genera, such as *Rhenopyrgus* indet. 1 and 3 (See Figs. 3.3-4, 6-7).

A striking feature of the contraction of the suboral constriction, in articulated rhenopyrgids, is that the oral surface is not withdrawn behind the collar plate circlet, only plates of the suboral contraction are obscured. This small retraction amounts to only 2-3mm. Smith and Jell (1990, fig. 53) reconstructed rhenopyrgids buried up to the oral surface, however, such a small retraction of the sub-oral constriction, on its own, seems insufficient to withdraw the oral surface sufficiently far into a burrow to make this mode of life a feasible suggestion, although its movement may have deterred some predators. It seems more likely that this contraction served to protect and cover the periproct (and other pores located within the suboral constriction). This must have been a particularly useful adaptation for deterring organisms entering these orifices if rhenopyrgids, as we think most likely, were epifaunal mudstickers with only the coriaceous sac inserted into the substrate (see below). The collar plates may also have been able to be partially withdrawn, as evidenced by the presence of processes on the aboral portions of these plates in *B. grayae* (Smith, 1985) and *R. flos* (Klug et al., 2008 plate 16 figs 1-14). Flexibility of the suboral constriction is apparent in numerous specimens and may have facilitated the redirection of the oral surface into more favourable positions within changeable currents, e.g. facing directly into a current to enhance feeding, disperse gametes or remove waste, as is observed in crinoids (Hess et al., 2004).

The pyrgate zone elevates the feeding structures higher up into the water column for more efficient filter feeding; a trend seen in other edrioasteroids (Sumrall and Sprinkle, 1990, Sprinkle and Sumrall, 2015). However, Klug et al. (2008) speculated that the imbricate nature of the pyrgate zone in rhenopyrgids enabled it to contract, withdrawing the animal into the safety of a burrow. Indeed, this withdrawal would be made even more effective when combined with the contraction of the suboral constriction outlined above. To support this view, Klug et al. (2008, text fig. 9a-c) illustrated two end members, one short and broad with shallowly inclined plates and the other elongate and thinner with steeply inclined plates, and an intermediate in a suite of specimens from the Emsian of Morocco, and speculated that the short broad variety were contracted individuals. They applied this same logic to specimens of *P. ansticei* Bather, 1915 (now classified as Rhenopyrgidae indet.). However, all these specimens show features of diagenetic crushing (during sediment compaction) rather than contraction; all specimens have disarticulated oral zones with isolated elements (cover and oral plates) pushed into the top of the pyrgate zone (see Klug et al., 2008, plate 16 figs. 3, 4 and 8, 9); no plates of the suboral constriction exposed, only the tips of the collar plates visible; many ‘contracted’ specimens are curved and; the plates of the pyrgate zone are not able to change inclination in life as they are fused in circlets of 4 plates (Sprinkle and Sumrall, 2015). As such, crushing is far more likely an explanation rather than these structures being able to contract in life.

There is little further evidence of stem contraction in other rhenopygid taxa. Despite localised contraction being apparent in the proximal and distal parts of the pyrgate zone of specimen E 62753 (*R.* indet. 1, Fig. 3.3, 4) which is preserved perpendicular to the sediment bedding, evidence for taphonomic crushing rather than an ability to contract is suggested by the oral surface being crushed and the suboral constriction being contracted. There is very little variation in the structure of the pyrgate zone of *R. piojoensis* specimens irrespective of position with respect to bedding or, if the suboral constriction is contracted or not (see Fig. 6 of Sumrall et al., 2013). Furthermore, several specimens of *R. viviani* (MPEP1126.1, EE 16642b and EE 15755) preserved perpendicular to the bedding, have crushed oral surfaces and contracted suboral constrictions but unaffected pyrgate zones, as one would expect if this zone could not contract (Figs. 2.1, 8). Thus, no specimens of rhenopyrgids unequivocally show a capability of being able to contract the plates of the pyrgate zone. Thus, if the pyrgate zone could not contract, then rhenopyrgids would be unable to sufficiently retract the oral surface into a burrow by just contraction of the suboral constriction to make a burrow dwelling lifestyle, as reconstructed by Klug et al. (2008) and Smith and Jell (1990), feasible.

The pyrgate zones of almost all rhenopyrgid taxa, however, display some degree of flexibility. Some suggest a great deal of flexibility, e.g. *R. coronaeformis*, *R. flos*, and *R.* sp. indet. 1 whilst other less so. This flexure of the pyrgate zone probably facilitated movement of the oral surface to more favourable positions within variable currents. We therefore conclude that the imbricate nature of the pyrgate zone was to facilitate flexure rather than contraction, as has been proposed for other echinoderms, such as the proxistele of solutans (Lefebvre et al., 2012).

Whilst no rhenopyrgid specimens have been found in-situ, the coriaceous sac of several taxa from widely differing environments of preservation (e.g. *R. cornaeformis* from the relatively deep black shales of the Hunsrück Slate to the shallow water limestones of the Jupiter Formation), at different geological times and paleogeographical provinces frequently show entire membranous sacs, which may be lobed and/or textured. *Heropyrgus disterminus* and possibly some others even had spine like extensions. The fact they are often entire suggests that they were not cemented to a hard substrate. However, the morphology is consistent with a mud sticking strategy, where the lobed morphology and textured surfaces would have anchored the organism firmly within soft to firm substrates. It is perhaps worth reiterating that we propose only the coriaceous sac was buried, not the pyrgate zone.

Based on all these observations, we created the idealised reconstruction in figure 5 to illustrate how we believe these animals would have appeared and behaved.

Conclusions

There is broader morphological variation in the construction of the oral surface within the Rhenopyrgidae than previously thought although this variation is similar to that seen in the other stalked edrioasterid families Cyathocystidae and Edrioblastidae. As such, it would seem that stalked edrioasteroids have all converged on a similar morphological solution and that this feature does not help elucidate any clear interrelationships between these edrioasterids.

Oral surface construction was generally robust in rhenopyrgids, particularly so in certain taxa where the interradial plates and ambulacral floor plates were fused into a single compound plate, with adaptations to resist crushing pressures (with equivalents seen in cyathocystids and derived edrioblastoids). More frequent loss of the oral structures during preservation, when compared to the pyrgate zone, is attributed to the fact that they were comprised of many moveable parts and were also supported by moveable plates of the suboral constriction.

The suboral constriction could contract behind the collar plates and this was done to protected the periproct and related orifices, whilst the small movement of the oral surface may have also disturbed potential predators. However, this contraction was insufficient to withdraw the oral surface behind the collar plates, and thus protection of the oral surface was not the primary function of the contraction.

The pyrgate zone was flexible but not contractile. This served to raise the oral surface into the water column and potentially re-orientate it (in conjunction with movement within the suboral constriction) to more advantageous positions.

Rhenopyrgids were epibenthic, firm or soft substrate stickers, not burrow dwellers or encrusters.

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Figures and figure captions

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Figure 2. *Rhenopyrgus viviani* n. sp. from Jupiter Formation, Telychian of Anticosti Island, Québec, Canada. **(1-9)** From Cybéle Member, Rock Pool Ledge site on Jupiter River **(1-3)** (Paratype MPEP 1126.1). **(1)** Lateral view of entire specimen. Note it is preserved perpendicular to bedding with flattened oral surface but undisturbed pyrgate zone. **(2)** Detail of oral surface; white arrows point to ridges on adambulacral margin of the oral ossicles, which accommodated cover plates; black arrow points to the ridged ambulacral floor that is presumably an extension of the interadial oral ossicle (coated with ammonium chloride); **(3)** Oral surface without ammonium chloride; again, black arrow points to ridged ambulacral floor; **(4)** Oral view of cover plates showing vestige of 2-1-2 ambulacral arrangement (Paratype EE 15752); **(5)** Lateral view, note lack of any floor plate sutures along adambulacral margin of oral plates (Paratype EE 15753); **(6-8)** Holotype (EE 16642). **(6)** Note changing morphology of pyrgate zone ossicles; **(7)** Detail of oral surface and sub-oral constriction. Black arrow points to anal pyramid composed of rod-like ossicles. White arrow points to triangular cross section of cover plates; **(8)** Holotype slab showing two individuals (Holotype on right); **(9)** Lateral view with a well preserved suboral constriction. Also note a change in morphology of pyrgate zone plates (Paratype EE 15754); **(10)** From Pavillon Member at Rivière aux Plats. Distal pyrgate zone and bulbous coriaceous sack-like holdfast comprised of small granular plates (Paratype EE 15756). Abbreviations: CL – collar plates, CP – cover plates, O – oral plate. All scale bars represent 1 mm.

Figure 3. Rhenopyrgidae. All whitened with ammonium chloride **(1,2)** *Rhenopyrgus grayae* comb. nov. Upper Ordovician, Lady Burn Starfish Bed, Girvan, Ayrshire, Scotland (Holotype E23470). **(1)** Details of oral surface with prominent collar plates and apparently no suboral constriction. Black arrows highlight exposed floor plates in distal ambulacra. White arrow points to a small exposed part of a plate of the suboral constriction, suggesting that suboral constriction could be contracted behind collar plates. **(2)** Lateral view. **(3, 4)** *Rhenopyrgus* indet. 1, Silurian, Newland Formation, Newlands, Ayrshire, Scotland (E 62753). **(3)** Lateral view of pyrgate zone, arrow points to enlarged plates interpreted here as collar plates. **(4)** Oral view. Black arrow highlights disarticulated large D-shaped oral ossicle. **(5)** *Rhenopyrgus* indet. 2, Ordovician, Drummuck Series, Ardmillan, Girvan District, Ayrshire, Scotland (EE 16254). Lateral view of pyrgate zone. Note difference in size and morphology of the pyrgate ossicles suggesting it is different to *R. grayae* which is found in similar age rocks which are geographically close. Also note disarticulated ridged deltoid-shaped plate closely associated with articulated pyrgate plates. **(6–8)** *Rhenopyrgus* indet. 3 **(6-8)** Foulon Formation (middle Floian), La Croix de Roquebrun, Saint-Nazaire-de-Ladarez, Hérault, France (UCBL-FSL 713312). **(6)** Lateral view of whole specimen. **(7)** Enlargement of the oral surface, showing confused plate articulation of this region. Black arrow highlights possible oral ossicle. White arrows highlight collar plate series. **(8)** Late Tremadocian, beneath Saint-Chinian Formation, Saint-Chinian, SW of Donnadieu, Babeau-Bouldoux, Hérault, France (UCBL-FSL 713316). Lateral view. **(9-11)** *Rhenopyrgus coronaeformis* Rievers, 1961, Lower Devonian, Emsian, Hunsrück Slate, Bavaria, Germany (Holotype SNSB-BSPG 1958 XV 50). **(9)** Detail of oral surface and proximal structures. **(10)** Detail of oral surface. Note complicated cover plate articulation surfaces. Black arrow highlights grooved adambulacral margin of oral plate. **(11)** Detail of coriaceous sac. Abbreviations, O - oral plate. All scale bars represent 1 mm.

Figure 4. *Rhenopyrgus viviani* n. sp. Silurian (Lower Telychian), Jupiter Formation, Jupiter River, Anticosti Island, Canada. **(1)** Camera lucida of lateral CD ambulacral of holotype of *Rhenopyrgus viviani* n. sp. (EE 16642). Note periproct formed of small lath shaped plates adjacent to edge of oral plate. Also note lack of floor plates exposed along adambulacral margin of oral plate. **(2)** Camera lucida view of oral surface of paratype MPEP 1126.1. Note groove and ridge arrangement along adambulacral margin of oral plate which accommodated and held in place cover plates. Also note ridged surface of fused floor plates which may have accommodated tube feet. All scale bars represent 1 mm.

Figure 5. Idealised reconstruction of *Rhenopyrgus viviani* n. sp. Silurian (Lower Telychian), Jupiter Formation, Jupiter River, Anticosti Island, Canada. Note individuals with extended and contracted suboral constrictions and with only the coriaceous sac and very distal part of the pyrgate zone buried in the substrate. We contend that the peduculate zone was not able to contract but was flexible.

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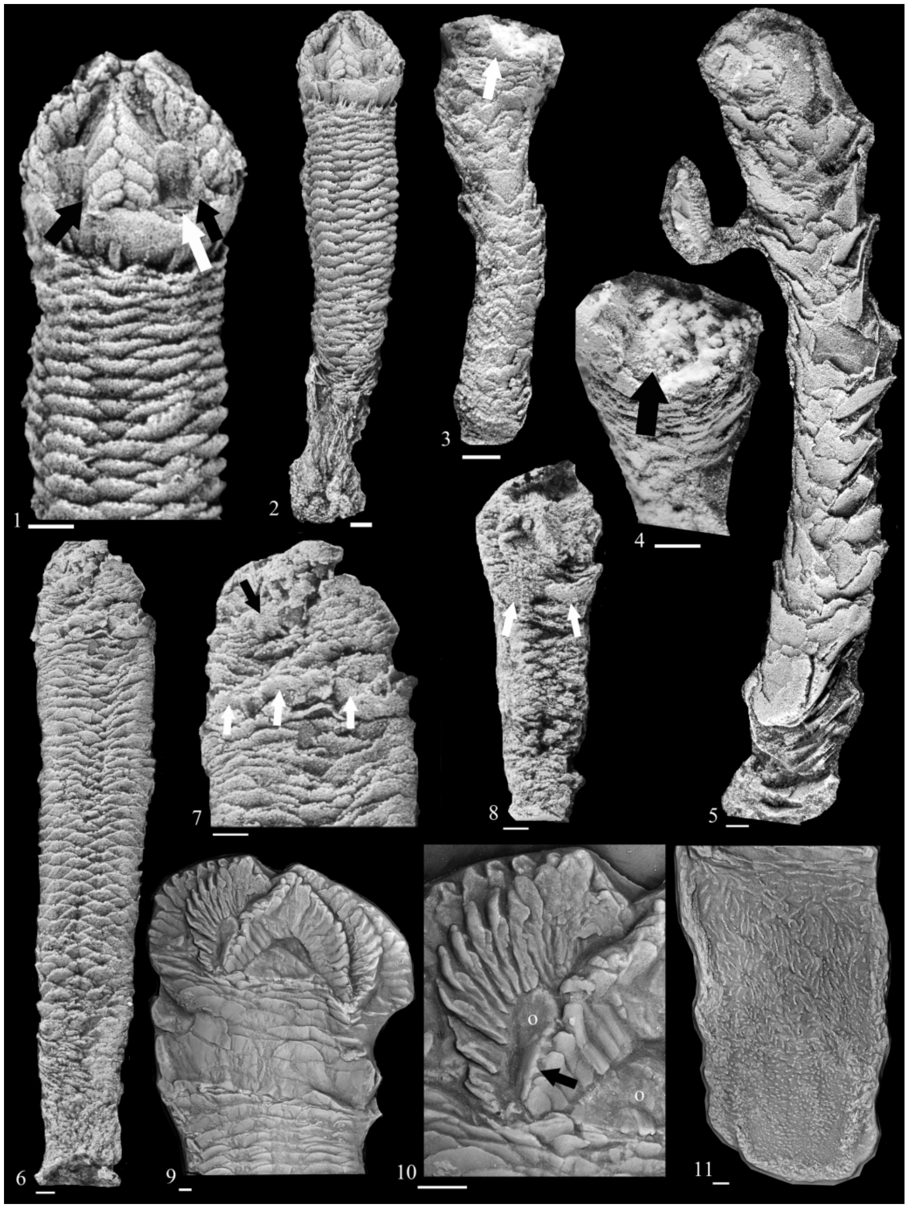

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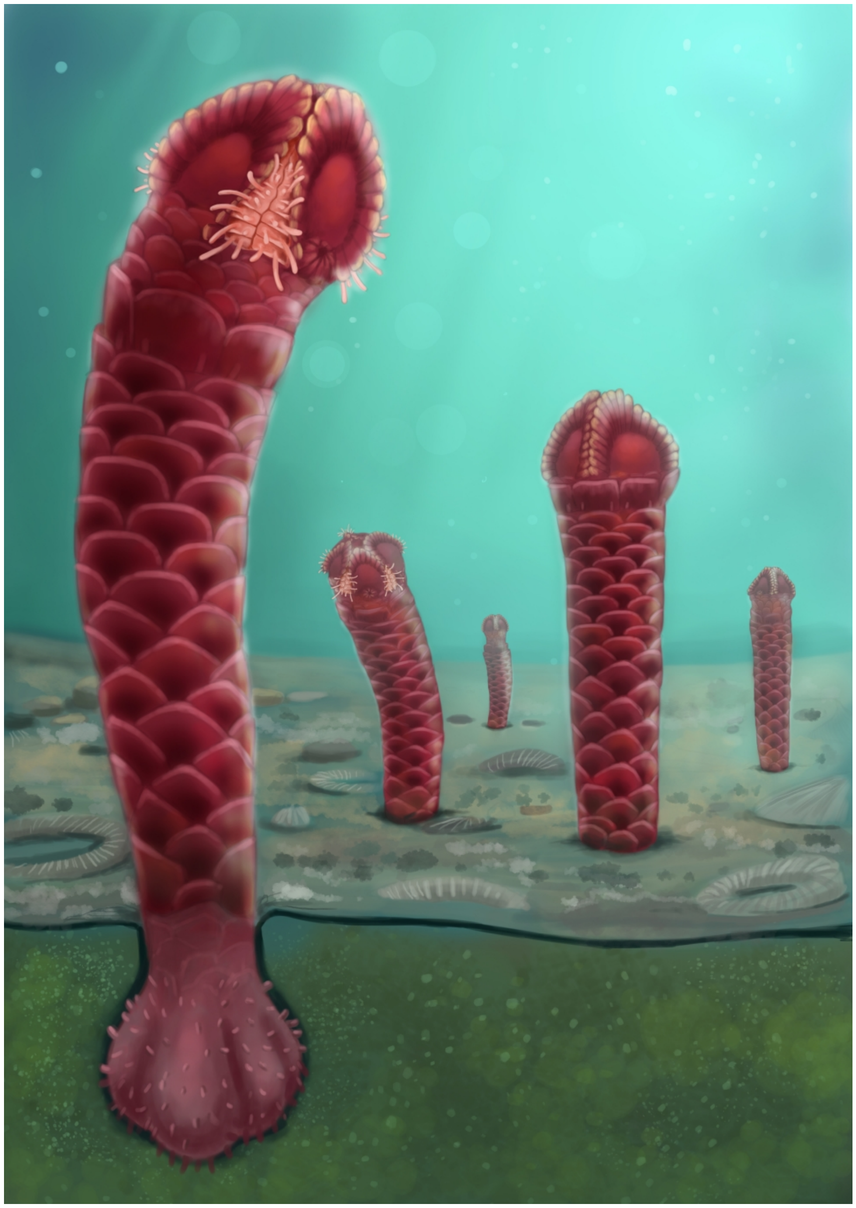

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