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Serpulid opercula (Annelida: Polychaeta) from the Upper Eocene of Possagno, NE Italy: taxonomy, taphonomy and palaeobiological significance

ROBERTO GATTO[1] & URSZULA RADWAŃSKA[2]

[1] *Dipartimento di Geologia, Paleontologia e Geofisica, Università di Padova, Via Giotto 1, I-35137 Padova, Italy.*
[2] *Institute of Geology, University of Warsaw, Al. Żwirki i Wigury 93, PL-02-089 Warszawa, Poland.*

ABSTRACT:

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A relatively rich assemblage of serpulid opercula (Polychaeta) is recognized, for the first time in Italy, in the Upper Eocene strata of the Possagno Marl exposed in the southern Alps (Province of Treviso, NE Italy). The studied material comprises four species referable to the genus *Pyrgopolon* DE MONTFORT, 1808. Of these, the new species *Pyrgopolon* (*Pyrgopolon*) *tubula* sp.n. is also present in the lower and middle Eocene deposits of north-western Europe, whereas *P.* (*P.*) *trochoides* (NYST, 1845) ranges from the middle Eocene to early Oligocene. The second new species, *Pyrgopolon cunialense* sp.n., is tentatively ascribed to the subgenus *Turbinia* MICHELIN, 1845. A common, or even a mass, occurrence of *Pyrgopolon* opercula in some Eocene/Oligocene sequences of western Europe is discussed. It is suggested that such an "opercular bloom" may have resulted from either taphonomic (selective transport and fossilization) or biologic (mass-shedding of opercula) factors, or a combination of both.

Key words: Polychaeta, Opercula, Palaeobiology, Taphonomy, Eocene, Italy.

INTRODUCTION

The aim of the present paper is to report on the finding of a relatively abundant assemblage of very rare fossils, namely the calcareous opercula of tube-dwelling polychaetes (family Serpulidae), recently discovered by one of the present authors (R.G.) in the Eocene marls exposed at Possagno, Province of Treviso, NE Italy. Though polychaete tubes have been extensively recorded in Italy, especially in the Cenozoic (*see e.g.*, ROVERETO 1898, 1904), polychaete opercula have not hitherto been recorded. The only report on Tertiary serpulid opercula in Italian monographs is that by ROVERETO (1904), who described, however, foreign material from France and Belgium.

A brief account of the studied subject was presented at the 13 Meeting of the Società Paleontologica Italiana, Parma 10-13 September 1996 (*see* GATTO & RADWAŃSKA 1996).

THE PROVENANCE OF THE STUDIED MATERIAL

The fossils studied come from the Possagno Marl cropping out near the village of Possagno. The Possagno Marl is a 550 to 600 metres thick marine sequence of Upper Eocene blue-grey, marly to silty clays, exposed on the northern flank of the foothills between Bassano del Grappa to the west and the Piave river to the east in the southern Alps (CITA 1968, 1975; BRAGA 1970). The formation can be subdivided into two units (TREVISANI 1997): a lower member represent-ed by about 450-500 metres of uniform clayey marl, rich in planktonic and benthonic foraminifera, and an upper member of upward increasingly silty clay, about 110 metres thick, with larger foraminifera and abundant macrofossils. This last part of the section, which yielded the studied material, belongs completely to the *Turborotalia cerroazulensis cunialensis* planktonic foraminifera Zone of TOUMARKINE & BOLLI (1975) and is therefore of Late Priabonian age. The Possagno Marl is overlain by the algal limestones of the Santa Giustina Limestone, also of Priabonian age (BRAGA 1972). Sedimentological and micropalaeontological evidence indicates that the shallowing upwards sequence of the Possagno Marl reflects a depositional environment gradually evolving from continental shelf to littoral (probably deltaic) conditions (CITA 1975; GRÜNIG & HERB 1980; TREVISANI 1997).

The Possagno area has long been considered a classic locality for the Paleogene strata in Europe. In the late 1960s it was visited during the *Colloque sur l'Eocène* (CITA & *al.* 1968), and the type-section of the Possagno Marl was proposed and accepted as parastratotype of the Priabonian stage (CITA 1969). Later, the stratigraphy and micropalaeontology of the Possagno succession, from the uppermost Cretaceous to Oligocene strata, were thoroughly reviewed in a monograph edited by BOLLI (1975). In 1980 GRÜNIG & HERB analyzed the stratigraphic distribution of benthonic foraminifera in the Possagno Marl, identifying five assemblage zones. These were interpreted as being related mainly to palaeobathymetric conditions, with water depth decreasing from about 1,000 m at the base of the formation to almost sea level at the top. More recently, in an attempt to calibrate precisely the Eocene/Oligocene boundary, volcano-sedimentary layers in the lower member of the Possagno Marl have been dated by means of radiometric methods at about 35 Ma (ODIN & *al.* 1991).

The blue-grey clays which constitute the upper member of the formation have been known to palaeontologists since the last century owing to their rich fossil contents, especially beautifully preserved corals and

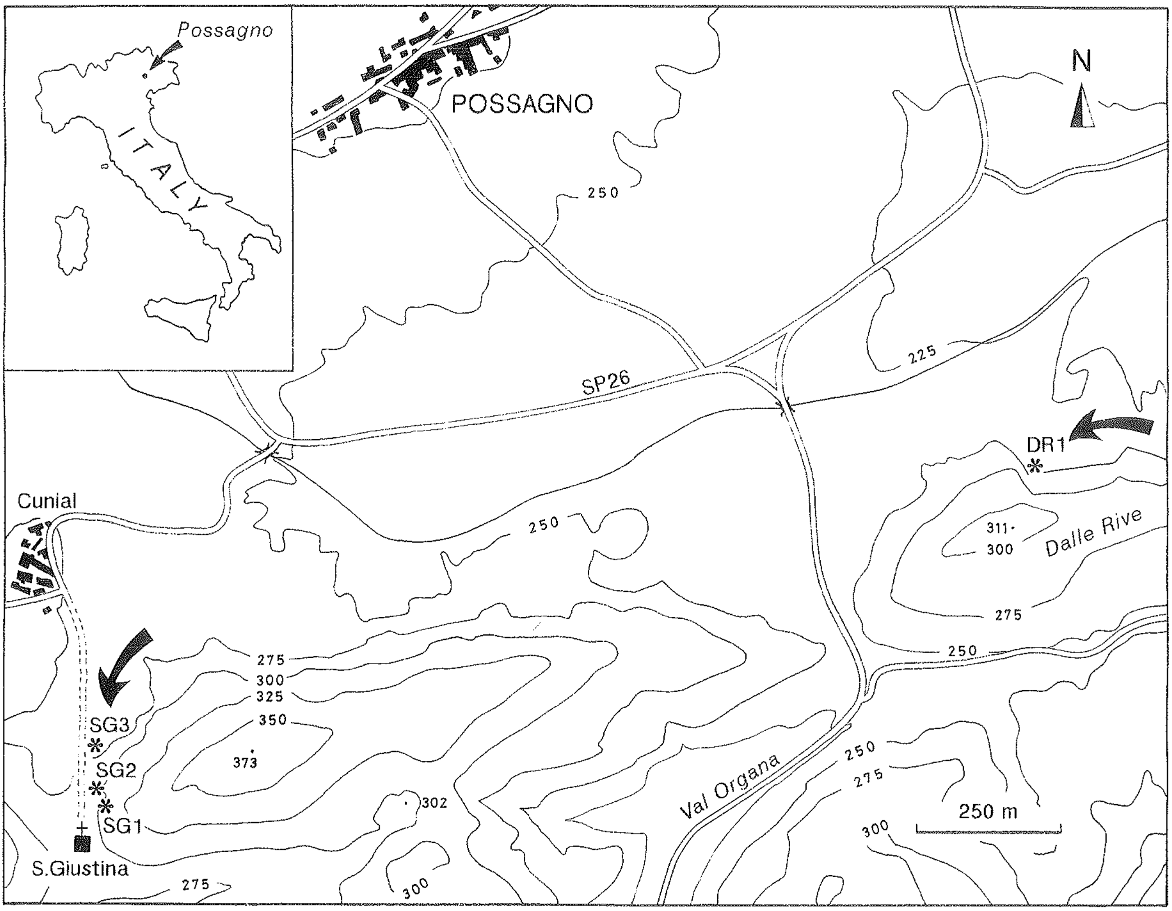

Fig. 1. Sketch-map of the Possagno area, to show the location of the samples (*arrowed*) yielding the studied serpulid opercula: samples *SG1*, *SG2*, and *SG3* from the Cunial Quarry (*see* Text-figs 2-3), sample *DR1* from "Dalle Rive"

Fig. 2. General view of the Cunial Quarry at Possagno (the village visible in the background), to show the exposure of the studied succession

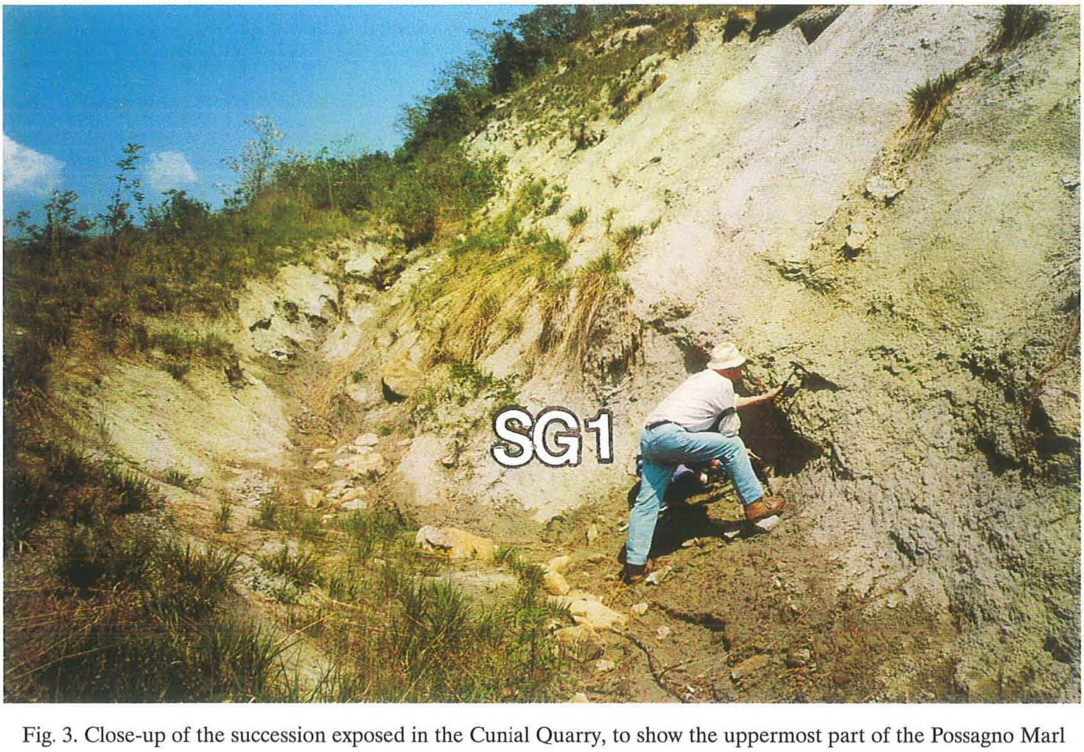

Fig. 3. Close-up of the succession exposed in the Cunial Quarry, to show the uppermost part of the Possagno Marl with the sampling site *SG1*

molluscs (D'ACHIARDI 1867; BAYAN 1870; ROSSI 1882; VINASSA DE REGNY 1897; OPPENHEIM 1901; RUSSO 1979). More recently they have also yielded vertebrate remains (BIZZARINI & *al.* 1977; BIZZOTTO 1983).

The opercular material described herein was collected from the upper member of the Possagno Marl exposed in two inactive quarries, south of the Possagno-Bassano provincial road (*see* Text-fig. 1). The first locality is the well-known Cunial Quarry at Possagno (*see* Text-figs 2-3), where CITA (1968) established the type-section of the Possagno Marl. Lithological description and stratigraphical sections of this exposure were given by CITA (1968, *and* 1975) and, more recently, by RUSSO (1979) and TREVISANI (1997). Three levels were sampled in this locality, *SG1*, *SG2* and *SG3* (from S. Giustina, a nearby chapel), respectively about 20, 35, and 85 m from the top of the formation. The second locality is the biggest of a series of quarries exposed along the SP26 road, 1.3 km SE of Possagno, very near the Val Organa section studied by GRÜNIG & HERB (1980). The level sampled (*DR1* from the toponym "Dalle Rive") is located about 30 m from the top of the formation, just below a conspicuous intercalation of indurated siltstones.

MATERIAL AND METHODS

A total of about 30 kg of clays were collected. After drying at 60° C for a week, the samples were immersed in a 5% solution of H_2O_2 for 24 hr. The disaggregated sediment was then washed, sieved through a 450 μm sieve and the resulting residues picked for opercula under a stereomicroscope. In total, 75 calcareous opercula were separated, including several fragmentary specimens. The opercula proved very fragile and the extracting process, though gently executed, almost invariably caused the loss of the stalk and often the breakage of the cup. For this reason the use of ultrasonic cleaning was avoided. Although tube fragments of serpulids were frequent in the samples collected, no operculum has been found *in situ*. All of the specimens examined in this study are housed in the *Museo di Geologia e Paleontologia* (MGPD) of the *Università di Padova*, Italy.

A GENERAL NOTE ON THE POLYCHAETE OPERCULA

In some present-day tube-dwelling polychaetes of the family Serpulidae RAFINESQUE, 1815, one of the filaments (radioles) of the branchial crown is modified to form an operculum which tightly closes the aperture of the habitation tube when the branchial crown is retracted.

Both the shape and structure of the opercula are very variable, and may differ considerably in particular genera and species, as shown, for example, by BIANCHI (1981) for the taxa inhabiting the Italian shorezones. For this reason they are extensively used as taxonomic characters, both at generic and specific levels, in the classification of the family (BIANCHI 1981). Usually the operculum consists of a proximal stalk, or peduncle, bearing a distal, variously shaped plug, normally strengthened by a chitinous or calcareous plate or cap. The operculum may bear sensorial organs (*e.g.* TEN HOVE 1973; TEN HOVE & NISHI 1996). Only some living Serpulidae possess a calcified operculum, the mineralization being normally restricted to the terminal plate. In other Serpulidae the terminal plate remains chitinous (*see e.g.* TEN HOVE & SMITH 1990). In a few genera the calcification is more pervasive, as for example in the fossil and Recent genus *Pyrgopolon* DE MONTFORT, 1808 (=*Sclerostyla* MØRCH, 1863), which has an entirely calcareous, funnel-shaped operculum (TEN HOVE 1973, TEN HOVE & NISHI 1996). The calcareous part of the operculum is intimately embedded in the filament cuticle tissue and in the living species *Pomatoceros lamarcki* (QUATREFAGES) is composed of aragonite (BUBEL 1973, 1983; THORP 1975; BUBEL & *al.* 1983). The fossil opercular caps, or *calottae*, described by one of the present authors (RADWAŃSKA 1994b), on the other hand, are calcitic.

Exceptionally, two opercula were reported to be functional in some species (*see* review and discussion by SCHOCHET 1973, p. 401). On the other hand, although nonfunctional pseudopercula are generally developed, the presence or absence of a functional operculum appears to be rather variable in some species of the present-day *Spiraserpula* REGENHARDT, 1961 (*see* PILLAI & TEN HOVE 1994, pp. 89 and 100).

A concise review of all of the hitherto recognized fossil opercula has recently been compiled by RADWAŃSKA (1994b), who also described for the first time opercular caps referable to some tubes of Middle Miocene (Badenian ≈ Langhian/Serravallian) age from the Korytnica Basin, in the southern slopes of the Holy Cross Mountains, Central Poland (RADWAŃSKA 1994a; *see also* TEN HOVE & NISHI 1996; ZIEGLER 1998, p. 38, Fig. 34).

The above-mentioned review (RADWAŃSKA 1994b, p. 85) shows that records of fossil polychaete opercula are still extremely scanty, and thus any new finds may significantly advance our knowledge of the biology and taxonomy of fossil polychaetes.

THE FOSSIL RECORD OF SERPULID OPERCULA

Given the fragile nature of these structure and their low preservational potential, it is not surprising that the fossil record of the opercula is much poorer than that of the tubes. The oldest opercula of the Serpulidae known so far are of Late Cretaceous age (*see* references in RADWAŃSKA 1994b, pp. 84-87). Perhaps the best known fossil opercula are the funnel-shaped forms, with a radiated upper disc, described from both Upper Cretaceous (WRIGLEY 1952; LOMMERZHEIM 1979; CUPEDO 1980b) and Paleogene deposits (NYST 1845; ROVERETO 1904; SCHMITT 1927; GERTH 1941; ALBRECHT & VALK 1943; WRIGLEY 1950, 1951; CUPEDO 1980b). These have usually been referred to the genus *Sclerostyla* MØRCH, 1863, a taxon recently shown by JÄGER (1993; *see also* JÄGER 1998) to be a junior synonym of *Pyrgopolon* DE MONTFORT, 1808. The entirely calcareous operculum of this genus is evidently more easily fossilizable than the less mineralized opercula of other serpulids and this condition may account for its widespread occurrence in the fossil record.

The genus *Pyrgopolon* DE MONTFORT, 1808, is especially common in the Eocene and Oligocene deposits of western Europe (particularly clays or claystones, and marls) where, intriguingly, the opercula seem to be more common than the tubes, a phenomenon that could be defined as an "opercular bloom". On the other hand, quite the reverse situation occurs in some Upper Cretaceous deposits of Europe, where the tubes of this genus are common but the opercula referable to it are absent (*e.g*, in the Chalk sequences, *see* RADWAŃSKA 1996). It is not easy to explain these situations at the moment, and it is only suggested that either taphonomic (selection during transport and burial) or biologic factors are to be taken into account.

Of the biological factors possibly responsible for the frequent, or even a mass, occurrence of polychaete opercula, attention should be focused on the ability of some present-day Serpulidae to shed their opercula and regenerate new ones. In the subfamily Spirorbinae, where this ability is more widespread, opercular moulting is a spontaneous activity: for example, opercular moulting and breeding cycles are strictly related in species which use the operculum as an incubation chamber for the eggs (THORP & SEGROVE 1975; and references therein). In the Serpulinae the process of opercular regeneration is probably induced by environmental factors, such as water disturbance, excessive (algal) overgrowth, or injury caused by predators. This was illustrated by SCHOCHET (1973) for the genus *Hydroides* GUNNERUS, 1768. In another genus, *Spirobranchus* BLAINVILLE, 1828, the phenomenon was reported by TEN HOVE (1994), who observed that specimens of *S. giganteus* (PALLAS, 1766) from Curaçao spontaneously shed their opercula and regenerated new ones when placed in an aquarium.

The discussed, still poorly known behaviour may be responsible for the production of numerous opercula by one individual of the polychaete which, on the other hand, is able to produce only one tube during its life, and it is known to die soon after when artificially removed (REGENHARDT 1961; JÄGER 1983; TEN HOVE & VAN DEN HURK 1993; TEN HOVE 1994). The "opercular bloom" found in some European Paleogene deposits may thus have resulted from such a mass-shedding (autotomy) of opercula induced either by some physical (? water disturbance) or biogenic (? predatory attacks, epidemics) factors. However, the phenomenon of autotomy and regeneration of the operculum has not hitherto been reported in the genus *Pyrgopolon*, to which the majority of the operculum-bearing species found in the Paleogene deposits belong, including those of Possagno. The production of more than one heavily-calcified operculum like that of *Pyrgopolon* by one individual may simply be too demanding in terms of energy.

On the other hand, various taphonomic processes may alternatively (or additionally) be responsible for the disparity in the opercula/tubes ratio of *Pyrgopolon* between different fossil assemblages. For example, it is reasonable to predict a selective hydrodynamic transport of the opercula, once these are liberated on the death of the polychaete and the tubes are still cemented to the substratum. In contrast, the presence of tubes with opercula *in situ* should imply a rapid burial. Furthermore, preservational bias may be invoked to explain the absence of opercula in those deposits where the tubes are common. Both mineralogy and microstructural architecture might account for a lower preservational potential of the operculum in comparison with the related tube. Unfortunately, while mineralogical composition and microstructure of serpulid tubes, both Recent and fossil, have been thoroughly studied (REGENHARDT 1961; BUBEL & *al.* 1983; VOVELLE & *al.* 1991, with references), the same cannot be said for calcified opercula, making an evaluation of these factors rather speculative.

The tubes of serpulids are mainly composed of calcite or aragonite or, to a smaller extent, a mixture of both (LOWENSTAM 1954; HEDLEY 1956; NEFF 1971; BORNHOLD & MILLIMAN 1973). The only published source on biomineralization in the opercula of living species is the already mentioned paper by BUBEL & *al.* (1983), who reported that the plate of *Pomatoceros* *lamarcki* (QUATREFAGES) was aragonitic, in contrast with the calcitic composition of the habitation tube. From a geochemical point of view, this makes the operculum more susceptible to dissolution than the tube. Unfortunately it is not known whether or not the aragonitic composition of opercular plates is a common condition in serpulids and further investigations on living species are evidently needed. To this purpose, a study to ascertain the mineralogy and microstructure of the operculum in fossil and Recent *Pyrgopolon* species is currently being carried out by one of the present authors (GATTO, *in prep.*).

Besides mineralogical composition, other intrinsic factors, such as the distribution of organic matter and porosity, combine to determine the resistance of skeletal remains to dissolution and maceration (ALEXANDERSSON 1978; CANFIELD & RAISWELL 1991; PARSONS & BRETT 1991; GLOVER & KIDWELL 1993). In this regard, BUBEL & *al.* (1983) made the interesting observation that in the opercular plate in *P. lamarcki* the organization of the organic matrix and the arrangement of the crystallites were more intimately correlated than in the habitation tube. This might imply that, as a result of decay of the organic matter on the death of the worm, the opercular plate becomes a porous structure more susceptible to dissolution (and maceration) than the tube.

However, albeit rarely preserved, the fossil opercular elements of serpulids may help to shed light on otherwise unknown palaeobiological aspects of their bearers, of which these elements sometimes represent the only remaining evidence. The occurrence of the opercula in the fossil assemblages may also provide additional information useful to reconstruct the taphonomic history of the once living polychaete community.

TAXONOMIC NOTES

The classification of fossil serpulids is necessarily based on the features of their habitation tubes. Admittedly, this contrasts with the neontologists' practice of evaluating characters such as soft parts, setae (= chaetae) and operculum (*see e.g.*, LOMMERZHEIM 1979, *and* JÄGER 1983). In fact, it has been observed in living species that the tube morphology can be greatly influenced by a number of environmental factors and that, conversely, different species can build almost indistinguishable tubes (TEN HOVE & VAN DEN HURK 1993). However, the palaeontological approach can hardly be expected to change substantially, though a more reliable taxonomic evaluation of the fossil species might result in the future from immunological studies of the organic matrix embedded in the structure of the tubes.

Morphological features of opercular parts are considered sound taxonomic characters in the living Serpulidae. Unfortunately, the low preservational potential and consequent rare fossil occurrence of opercula prevent using them routinely in the classification of extinct species. Moreover, fossil opercular elements (caps or opercula) are very rarely found in anatomical connection with the respective tubes. This circumstance makes problematical their attribution to taxa based on tubes only, and the possibility exists that the operculum and tube of the same species, if found separately, would be attributed to different nominal taxa. As an example, *Serpula instabilis*, introduced by WRIGLEY (1952) for some Upper Cretaceous isolated opercula, proved to be a synonym of *"Sclerostyla" ciplyana* (DE RYCKHOLT, 1852), after CUPEDO (1980b) who found the tubes of this last species with opercula *in situ*. Since all opercula described in the present paper were found loose, there is no possibility of ascertaining to which tubes they belonged. Therefore, to avoid making speculative conclusions, no tube references are included in the synonymy lists given below.

In an often cited paper of 1951, WRIGLEY thoroughly described some Eocene and Oligocene European species of *"Sclerostyla"* and allied genera, also illustrating opercula ascribable to them. Although differences between opercula were noted, he did not regard them as taxonomically significant and preferred to distinguish the species on the basis of tubes alone, stating that the opercula "... give no firm grounds of specific distinction..." (WRIGLEY 1951, p. 186). The present authors do not agree with WRIGLEY's assumption and believe that differences in opercular features (*i.e.* general shape of cup and peduncle, sculpture of upper surface and pattern of grooves) should be considered, when possible, in evaluating fossil species, giving them equal, if not greater value than those of tube characters, as in the present-day species. In fact, in some recently published papers (*e.g.*, NISHI & ASAKURA 1996) the opercula make up the majority of the description and illustration of the species studied.

SYSTEMATIC ACCOUNT

Class **Polychaeta** GRUBE, 1850
Order **Sedentarida** LAMARCK, 1818
Family **Serpulidae** RAFINESQUE, 1815*

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* This authorship is given herein, to follow the treatment by JÄGER (1993, p. 74), and used formerly by one of the present authors (RADWAŃSKA 1994a, p. 40).

Subfamily **Serpulinae** MacLeay, 1840

Genus *Pyrgopolon* de Montfort, 1808
Type species: *Pyrgopolon mosae* de Montfort, 1808

For a comprehensive revision of the genus *see* Jäger (1993).

Subgenus *Pyrgopolon* de Montfort, 1808

Pyrgopolon (*Pyrgopolon*) *tubula* sp.n.
(Plate 1)

1904. *Serpula* (*Sclerostyla*) *Mellevillei* Nyst et Le Hon; G. Rovereto, p. 24, Pl. 3, Fig. 10k (*non* Nyst & Le Hon 1862).
partim 1927. *Serpula heptagona*, v. Hag.; W. Schmitt, p. 138, Pl. 10, Figs 1-3 and 9 (*non* von Hagenow 1840); *non* Figs 4-5 [=*Pyrgopolon* (*Turbinia*) *abbreviatum* (Deshayes, 1825)].
1950. *Serpula* Sp. *1*; A. Wrigley, p. 503, Text-figs 4a-4b.
?1951. *Sclerostyla trochoides* (Nyst); A. Wrigley, p. 188, Text-fig. 47.

HOLOTYPE: The specimen MGPD 28718 from sample *DR1*, figured in Pl. 1, Figs 1-3.

PARATYPES: Two specimens: MGPD 28719 figured in Pl. 1, Figs 4-5, and MGPD 28720 figured in Pl. 1, Figs 6-8, both from sample *SG2*.

TYPE LOCALITY: Quarry in locality "Dalle Rive", 1.3 km SE of Possagno (Province of Treviso, NE Italy).

DERIVATION OF THE NAME: Latin *tubula* – small trumpet, referring to the shape of the operculum.

DIAGNOSIS: Cup acutely conical, upper side deeply concave with relatively few (14-21) straight, radial ridges. Radial ridges low and thick, inversely *V*-shaped, in some cases covered by tubercles. Margin of the cup undulated by rounded teeth. Cup tapering gently into the peduncle. Peduncle inserted eccentrically (more ventrally) into the cup, with one ventral and two lateral longitudinal grooves.

DESCRIPTION: The cup is acutely conical, deeply concave on the upper side, ranging in diameter from 0.69 to 1.02 mm, with relatively few, widely spaced, straight radial ridges on it. The number of the radial ridges varies from 14 to 21. All of the ridges are low and relatively thick, smooth or covered by tubercles (*see* Pl. 1, Figs 3-4, 6), inversely *V*-shaped in cross-section. The ridges are long and continue to the centre of the cup (*see* Pl. 1, Figs 3-4, 6). The margin of the cup (*see* Pl. 1, Figs 1-2, 5, 8) bears rounded teeth, corresponding to the ridges. The lower surface of the cup (*see* Pl. 1, Figs 1-2) is covered by a network of wide, branching grooves and, in the uncorroded specimen (*see* Pl. 1, Figs 7-8), by irregularly arranged tubercles. The cup gradually passes into the peduncle, which is inserted eccentrically (more ventrally) into the cup (*see* Pl. 1, Figs 1-2). The peduncle has one ventral and two lateral, longitudinal grooves. The ventral groove is deeper than the lateral ones (*see* Pl. 1, Figs 1-2, 7; *also* sketch-drawing in Pl. 1). The cross-section of the peduncle is subquadrangular (*see* Pl. 1, Fig. 7; *also* sketch-drawing in Pl. 1). The proximal end of the peduncle is not preserved in the material examined.

REMARKS: The synonymy list of this new species includes the operculum described by Rovereto (1904) from the Eocene deposits of Saint Gobain (Paris Basin), and classified as *Serpula* (*Sclerostyla*) *Mellevillei* Nyst & Le Hon. In 1950 Wrigley regarded this specimen as conspecific with those coming from the "base du Calcaire grossier" in several localities of the Paris Basin and at Bois-Gouët in Brittany that he named "*Serpula* Sp. *1*". He stated that these opercula, distinguishable by the low angle of the cup and its very gradual transition to the peduncle, did not belong to Nyst & Le Hon's *mellevillei*. The following year, describing the Eocene material from England, Wrigley (1951) reported that similar opercula, having a "...reticulate cone of a much smaller angle than in the Barton form" (that is, "*Sclerostyla*" *mellevillei*), were present also in the Lutetian Bracklesham bed at Southampton; he suggested that they might be referred to a separate species, though he did not name it, the related tube being unknown. This type of operculum had also been recorded from Barisis au Bois, in the Paris Basin (probably from the Sables de Cuise) by Schmitt (1927), who erroneously ascribed it to *Serpula heptagona* von Hagenow, 1840 [= *Pyrgopolon macropus* (Sowerby, 1829)]. However, part of Schmitt's material (1927, Pl. 10, Figs 4-5) really belongs to *Turbinia* Michelin, 1845 (a subgenus of *Pyrgopolon* according to Jäger 1993), as recognizable from the small size, and the upward stacking concentric growth zones on the cup (*see* Michelin 1845; Wrigley 1950, 1951).

Interestingly, Wrigley (1951) listed Schmitt's *heptagona* among the synonyms of a new established species, *Sclerostyla gallica*. This taxon, whose material also comes from Barisis au Bois, is difficult to evaluate, as its diagnosis was based on tube morphology alone. The opercula associated with it were poorly figured and it is not clear whether they were found *in situ*. Indeed Wrigley stated that the opercula of *gallica* "...have all the characters described for *S. mellevillei*, the angle of the cone being variable". However, this author probably included in *gallica* opercula belonging to different species, on the clearly expressed assumption that opercular characters are of less taxonomic value than tubes.

The new taxon here established shows rather constant and easily distinguishable characters and therefore it seems safer to keep it separate from other *Pyrgopolon* species.

DISTRIBUTION: The species is known from the upper Ypresian and Lutetian of the Paris Basin, France, the Lutetian of the Hampshire Basin, England, and Brittany, France, and the upper Priabonian of the Possagno area.

Pyrgopolon (*Pyrgopolon*) *trochoides* (Nyst, 1845)
(Plates 2-4)

1845. *Cyclolites trochoides* Nob.; P.-H. Nyst, p. 634, Pl. 15, Fig. 12.
? 1862. *Galeolaria* (*Cyclolites*) *trocoides* (sic!) Nyst; H. Le Hon, p. 827.
? 1868. *Galeolaria* (*Cyclolites*) *trochoides* Nyst; P.-H. Nyst *in* G. Dewalque, p. 407.
1868. *Galeolaria* (*Cyclolites*) *trochoides* Nyst; J. Bosquet *in* G. Dewalque, p. 416.
1872. *Galeolaria* (*Cyclolites*) *trochoides*; T. Lefevre & G. Vincent, p. 12.
? 1904. *Serpula* (*Sclerostyla*) *Mellevillei* Nyst et Le Hon var. *trochoides*; G. Rovereto, p. 25, Pl. 3, Fig. 10f.
? 1927. *Serpula*; W. Schmitt, p. 140, Pl. 10, Figs 8-9.
1941. *Cyclolites trochoides*; H. Gerth, p. 160, Text-fig. 2.
1951. *Sclerostyla mellevillei* (Nyst and le Hon); A. Wrigley, p. 185, Text-fig. 37.
non 1951. *Sclerostyla trochoides* (Nyst); A. Wrigley, p. 188, Text-fig. 47 [see *P.* (*P.*) *tubula*].
1980b. *Sclerostyla mellevillei* Nijst et le Hon; F. Cupedo, p. 4, Text-figs 1, 3, 16.

MATERIAL: Six specimens from sample *DR1* (MGPD 28721), 9 specimens from *SG1* (MGPD 28722), 7 specimens from *SG2* (MGPD 28723), 9 specimens from *SG3* (MGPD 28724).

DESCRIPTION: The cup, ranging in diameter from 0.88 to 2.81 mm, is conical (*see* Pl. 2, Figs 3-4; Pl. 3, Figs 1, 7-8; *and* Pl. 4, Figs 2-3), moderately concave on the upper side, which is covered by relatively few, straight, radial ridges. The radial ridges are relatively high and short and do not reach the centre of the cup. They are inversely *V*-shaped in cross-section, with rather spaced, irregular, long spines. These are gently curved towards the centre of the cup (*see* Pl. 2, Figs 3-6; Pl. 3, Figs 2, 4; Pl. 4, Figs 3, 7). The number of ridges varies from 17 to 23. They are separated by shallow and wide, concave grooves. Some faint circular, concentric growth rugae are also present on the upper side of the cup. These are more evident on the central area which is devoid of radial ridges. The outer margin of the cup bears a number of sharply pointed teeth, corresponding to the ridges (*see* Pl. 2, Figs 2-5; Pl. 3, Fig. 5; Pl. 4, Figs 4-5). The lower surface of the cup is covered by a network of irregularly and closely branching grooves (*see* Pl. 2, Fig. 1 and Pl. 3, Fig. 3). These are more developed near the peduncle insertion and fade towards the outer margin of the cup, becoming radially directed. Here the grooves are deeply incised in coincidence with the marginal teeth, making the edge of the cup indented. The peduncle, inserted almost centrally or slightly ventrally to the cup, is long, and sculptured by four longitudinal grooves (*see* Pl. 2, Figs 1-3; *also* sketch-drawing in Pl. 2), of which the dorsal one is short and wide, and covered by small, delicate ridges. The two lateral grooves are long and shallow, whereas the ventral one is deep, long, and moderately wide. The lateral and ventral grooves pass into the network of grooves on the lower surface of the cup (*see* Pl. 2, Figs 1-2 and Pl. 3, Fig. 3). The peduncle is laterally compressed, and its base is *S*-shaped (*see* Pl. 3, Fig. 6). The cross-section of the peduncle is oval (*see* the sketch-drawing in Pl. 2).

REMARKS: The taxon *Pyrgopolon* (*P.*) *trochoides* is one of the first fossil polychaete opercula described in palaeontological literature. Nyst (1845), who initially misinterpreted it as a cnidarian, recorded the species from the Tongrian of Lethen and Vliermael in Belgium (now respectively Leten and Vliermaal).

Some confusion exists about the correct name for the polychaete species to which this operculum belonged. Most authors assumed that the related tube is "*Serpula*" *mellevillei*, established by Nyst & Le Hon (1862) from the Laekenian (Middle Eocene) of Belgium (Lefevre & Vincent 1872; Rovereto 1904; Gerth 1941). This seems to be in conflict with Nyst (*in* Dewalque 1868, p. 409), who stated that the operculum of *mellevillei* was the coeval *Galeolaria* (*Cyclolites*) *trochiformis* Nyst (apparently a *nomen nudum*), while ...*Galeolaria trochoides*, du Tongrien, "n'est qu'un opercule semblablé" (to add confusion, *G. trochiformis* is spelled "*trochoides*" on p. 407 of the same paper). The

Middle Eocene species *mellevillei*, common also in the English Bartonian, was kept separate from the younger *trochoides* by WRIGLEY (1951), on the basis of the tube microstructure. However, the identification of *trochoides* made by this author is doubtful, as the operculum figured by him clearly differs from that of NYST because of its very gradual transition between cup and peduncle. On the other hand, WRIGLEY's illustration of a Bartonian operculum ascribed to *mellevillei* does agree well with the original illustration of *trochoides* provided by NYST.

Though very probable, the synonymy between *trochoides* and *mellevillei* is difficult to ascertain, since the first taxon was established on the operculum and the second on the tube. Unfortunately, the absence of well preserved material comprising tubes and opercula *in situ* makes a definite statement about the two taxa impossible at present.

The operculum of *Pyrgopolon* (*P.*) *trochoides* is close to those of the two present-day species, *P. ctenactis* (MØRCH, 1863) and *P. semiannulatum* (TEN HOVE, 1973), which are known from the Caribbean (*see* TEN HOVE 1973). It differs, however, in its shallower cup, widely spaced and shorter ridges, a better developed network of grooves on the lower surface of the cup, and in the *S*-shaped base of the peduncle.

The preservation of the investigated material is variable. Two specimens have their outer layer well preserved, and thus a deep network of grooves on the lower surface of the cup is clearly observable (*see* Pl. 2, Fig. 1 and Pl. 4, Figs 6, 8). In other specimens, devoid of the outer layer, the surface of the cup is almost smooth or sculptured by shallow grooves (*see* Pl. 2, Fig. 2; Pl. 3, Fig. 5 and Pl. 4, Figs 1, 4).

DISTRIBUTION: Besides being present in the upper Priabonian of Possagno, *P.* (*P.*) *trochoides* has been found in the lower Rupelian of Belgium, the Netherlands and possibly Germany, and in the Bartonian of the Hampshire Basin (England).

Pyrgopolon (*Pyrgopolon*) sp.
(Plates 5-6)

MATERIAL: Five specimens from sample *SG1* (MGPD 28725).

DESCRIPTION: The cup is low-conical (*see* Pl. 5, Figs 1, 4; *and* Pl. 6, Figs 1-4, Figs 8-9), ranging in diameter from 1.32 to 2.43 mm, with numerous straight, radial, well developed ridges on the flat upper side. The ridges, the number of which varies from 36 to 41, are arranged in two or more alternating series of different length, none of which reaches the centre of the cup. The centre of the cup is therefore devoid of ridges. All ridges are low, inversely *V*-shaped in cross-section, and covered by closely spaced tubercles (*see* Pl. 5, Fig. 1, 4-6 and Pl. 6, Figs 5-6). The cup growth lines are circular and eccentrically developed (*see* Pl. 5, Fig. 1 and Pl. 6, Figs 3, 5). The outer margin of the cup (*see* Pl. 5, Figs 2, 4 and Pl. 6, Figs 2, 4) bears numerous sharp teeth, formed by the distal ends of the radial ridges. The lower surface of the cup (*see* Pl. 5, Fig. 3 and Pl. 6, Figs 2, 7) is regularly sculptured by radially arranged shallow grooves which coincide with the upper ridges. The grooves branch irregularly on the peduncle insertion. The peduncle is inserted eccentrically and passes rather gradually to the cup (*see* Pl. 5, Fig. 4 and Pl. 6, Figs 1, 9). Although the peduncles are broken in all specimens, on the preserved fragments three grooves are observable: one ventral and deep, and two lateral and shallow (*see* Pl. 5, Fig. 3 and Pl. 6, Fig. 9; *see* also sketch-drawing in Pl. 5). The peduncle cross-section is oval or subquadrangular (*see* Pl. 5, Fig. 3; *see* also sketch-drawing in Pl. 5).

REMARKS: The collected specimens are close to those of the preceding species *Pyrgopolon* (*P.*) *trochoides* (NYST, 1845). They differ, however, in the flat upper side of the cup, the almost double number of ridges, which are generally shorter, and in the more eccentric growth of the cup.

Because of the lack of well preserved specimens (the outer surface is corroded and basal parts of the peduncle are missing), the studied material can be determined only to genus level.

DISTRIBUTION: Found only in the upper Priabonian of the Possagno area.

Subgenus *Turbinia* MICHELIN, 1845

Pyrgopolon (*Turbinia*?) *cunialense* sp.n.
(Plates 7-8)

HOLOTYPE: The specimen MGPD 28726 from sample *SG2*, figured in Pl. 7, Figs 1-3.

PARATYPES: Four specimens from sample *DR1*: figured in Pl. 7, Fig. 4 (MGPD 28727); Pl. 7, Figs 5-6 (MGPD 28728); Pl. 8, Figs 1-3 (MGPD 28729); Pl. 8, Fig. 10 (MGPD 28730); two specimens from *SG1*: figured in Pl. 8, Figs 4-5 (MGPD 28731); Pl. 8, Figs 6-7 (MGPD 28732) and one specimen from *SG3*: figured in Pl. 8, Figs 8-9 (MGPD 28733).

TYPE LOCALITY: Cunial Quarry, Possagno (Province of Treviso, NE Italy).

ADDITIONAL MATERIAL: Nine specimens from sample *DR1* (MGPD 28734), 8 specimens from sample *SG1* (MGPD 28735), 12 from *SG2* (MGPD 28736), 9 from *SG3* (MGPD 28737).

DERIVATION OF THE NAME: The species is named after its type locality.

DIAGNOSIS: Cup low-conical, upper side almost flat with numerous (36-46), straight, radial ridges. Radial ridges relatively low, inversely *U*-shaped in cross-section, alternately reaching almost the centre of the cup. Outer margin of the cup forming a characteristic thick band, characterized by numerous, regularly spaced teeth that gives it the appearance of a pinion or cogwheel. Peduncle eccentrically (more ventrally) inserted into the cup, with four longitudinal grooves. Ventral side of the peduncle with a deep, wide groove, gradually passing into the cup. Dorsal side with a shallow groove, passing into the cup at almost a right angle. Cross-section of the peduncle subtriangular.

DESCRIPTION: The cup is low-conical, ranging in diameter from 0.87 to 1.36 mm, slightly swollen ventrally, with a shallow or almost flat upper side. In some cases there is a well defined, depressed central area or a raised, concentric disc of smaller diameter (*see* Pl. 7, Figs 1-2, 6; and Pl. 8, Figs 2-7). The upper side is covered by relatively low, straight, radial ridges, inversely *U*-shaped in cross-section (*see* Pl. 7, Figs 2, 6; and Pl. 8, Figs 3, 7, 9). The ridges are numerous, their number varying from 36 to 46. They are of different length, alternately longer and shorter, the longer ones being slightly higher and almost reaching the centre of the cup. The edge of the cup (*see* Pl. 7, Figs 1, 4-5; and Pl. 8, Figs 1, 5-6, 8, 10) is characteristically thick, sculptured like a bevel pinion (cogwheel), with numerous regularly spaced vertical teeth extending radially from the under side. The teeth are in some cases connected to each other near their upper end to form a continuous ring around the edge of the cup. The distal ends of the upper radial ridges also form a series of short and blunt teeth on the margin of the upper side, which alternate with those underneath. The lower surface of the cup (*see* Pl. 7, Figs 3-4; and Pl. 8, Figs 1, 8) is smooth or covered by an irregular network of weakly incised, branching grooves. The peduncle is probably long (entire peduncle is not preserved) and eccentrically inserted to the cup (*see* Pl. 7, Figs 1, 5; and Pl. 8, Figs 5, 10). The insertion is very characteristic: on the ventral side the peduncle passes gradually into the cup, expanding ventro-laterally in two diverging, connected branches, whereas on the dorsal side it meets the cup at almost a right angle (*see* Pl. 7, Figs 1, 4). The peduncle is incised by four longitudinal grooves. One of them runs ventrally and is deep and wide, while the others, two lateral and one dorsal, are shallow (*see* Pl. 8, Figs 5, 10; *also* sketch-drawing in Pl. 7). The cross-section of the peduncle is subtriangular near the insertion to the cup (*see* Pl. 7, Fig. 3; *also* sketch-drawing in Pl. 7), becoming subquadrate more proximally.

REMARKS: The overall shape of these opercula, with a conical cup and a rod-like peduncle, is typically that known in the genus *Pyrgopolon*. However, the thick, denticulate band on the margin of the cup is a character shared with the opercula referred to *Turbinia* MICHELIN, 1845 (here lowered to subgeneric status following JÄGER 1993). However, in the known species ascribed to *Turbinia* the teeth forming the marginal band are a prolongation of the upper radial ridges (*see* WRIGLEY 1950, p. 500), whereas in the studied species they alternate with them. Further distinguishing characters are the upper side of the cone which, though sometimes composed of two superimposed discs, is never convex as in *Turbinia*; and the peduncle insertion with expanding branches. A similar peduncle insertion is found among the members of the subgenus *Hamulus* MORTON, 1834. In *Hamulus*, however, the peduncle consists of three distinct flanges fused along their inner margin, and its cross-section is distinctly *T*-shaped rather than triangular, as seen, for example, in *Pyrgopolon* (*Hamulus*) *sexcarinatum* (GOLDFUSS, 1841) figured by CUPEDO (1980a).

In the present authors' opinion, the features of the studied Possagno specimens are sufficient to establish a separate species, although its subgeneric assignment cannot be determined unequivocally.

DISTRIBUTION: Found only in the upper Priabonian of the Possagno area.

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PLATES 1 – 8

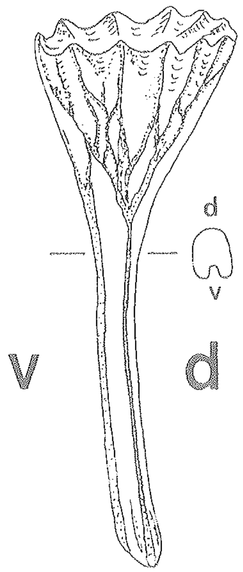
PLATE 1

Pyrgopolon (*Pyrgopolon*) *tubula* sp.n.

Sketch-drawing shows the reconstruction of a complete operculum in left lateral view, and a cross-section of the peduncle; **v** – ventral side, **d** – dorsal side

1-3 – **Holotype**, MGPD 28718: 1 – Oblique left lateral view, 2 – Left lateral view, 3 – Top view of the cup
4-5 – **Paratype**, MGPD 28719: 4 – Oblique top view, 5 – Right lateral view
6-8 – **Paratype**, MGPD 28720: 6 – Oblique top view, 7 – Oblique outer view, 8 – Left lateral view

All specimens from the Possagno Marl, Possagno



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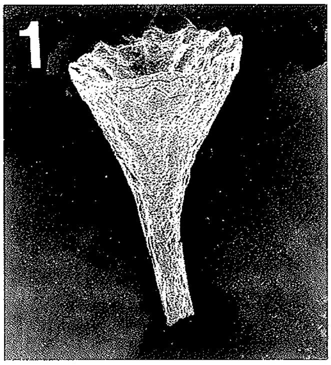

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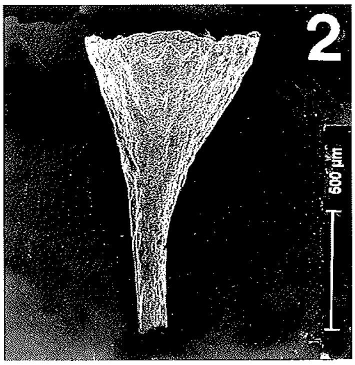

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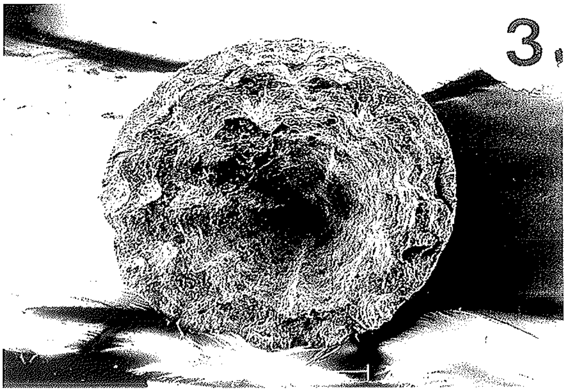

Pyrgopolon (*Pyrgopolon*) *tubula* sp.n.

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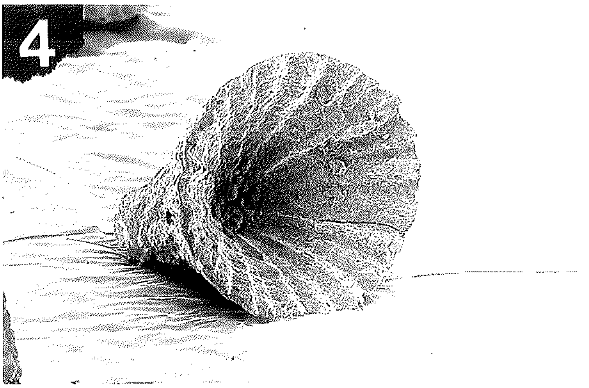

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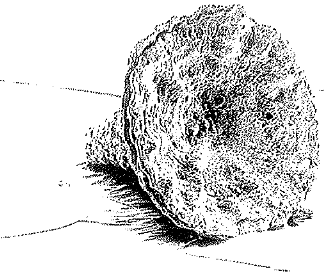

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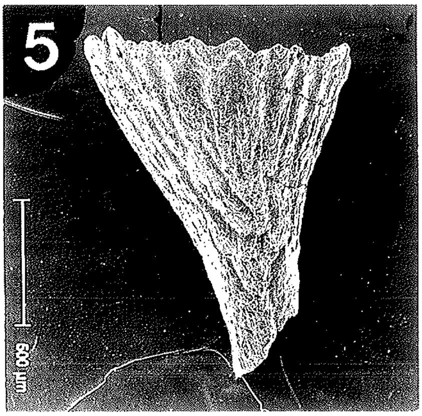

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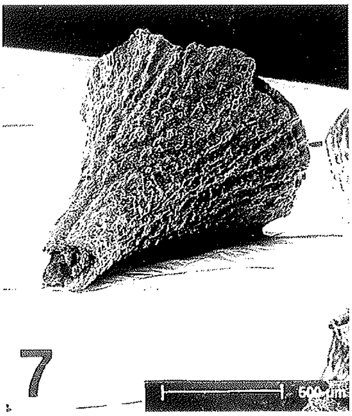

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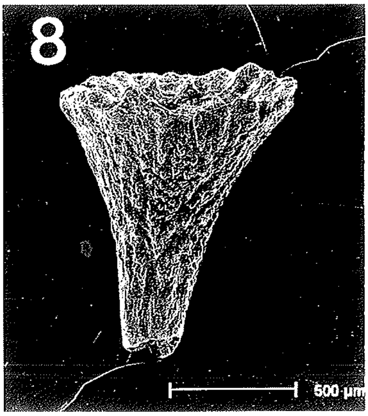


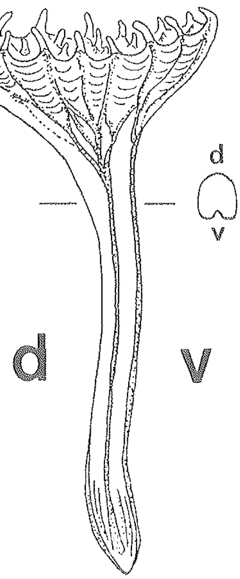
PLATE 2

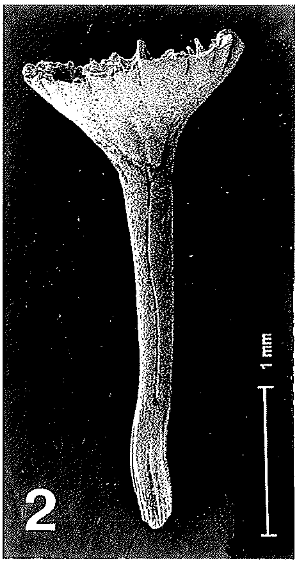
Pyrgopolon (*Pyrgopolon*) *trochoides* (NYST, 1845)

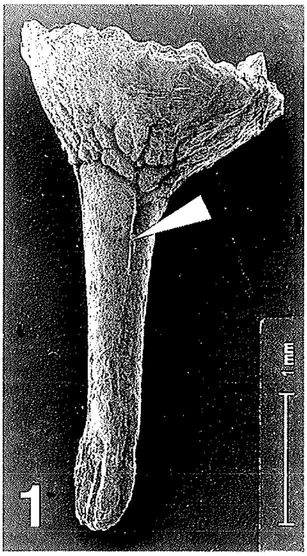
Sketch-drawing shows the reconstruction of a complete operculum in right lateral view, and a cross-section of the peduncle: **d** – dorsal side, **v** – ventral side

1 – Specimen in oblique view (MGPD 28722/1), to show the ventral groove (*arrowed*)
2-6 – A partly exfoliated specimen (MGPD 28724/1): 2 – Right lateral view; 3 – Oblique top view, to show lateral (*l*) and ventral (*v*) grooves of the peduncle; 4 – Top view of the cup; 5-6 – Close-up views of the cup, to show the structure of the spines

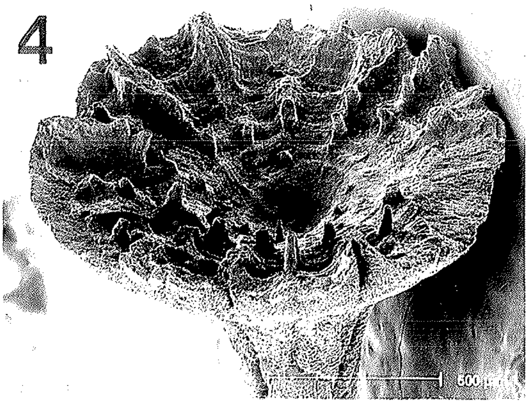
All specimens from the Possagno Marl, Possagno

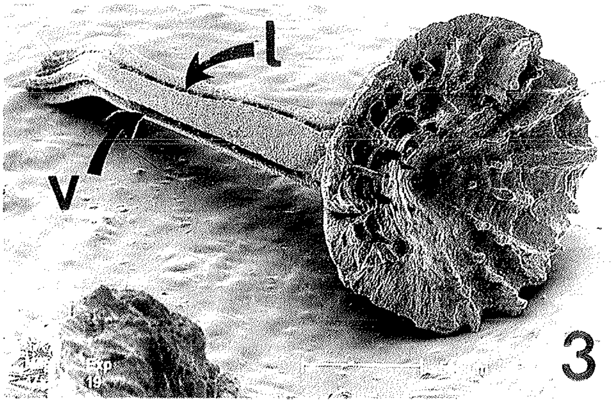






Pyrgopolon (*Pyrgopolon*) *trochoides* (NYST, 1845)





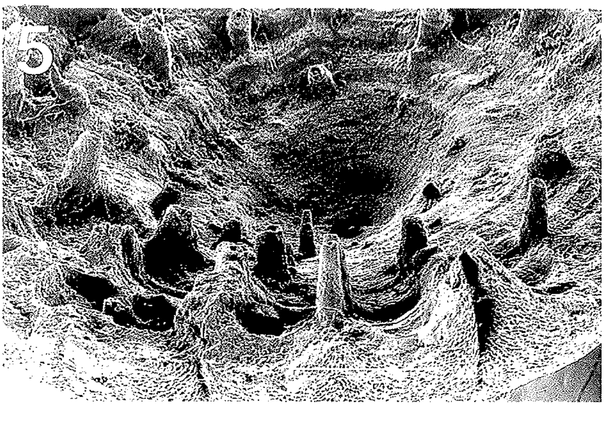
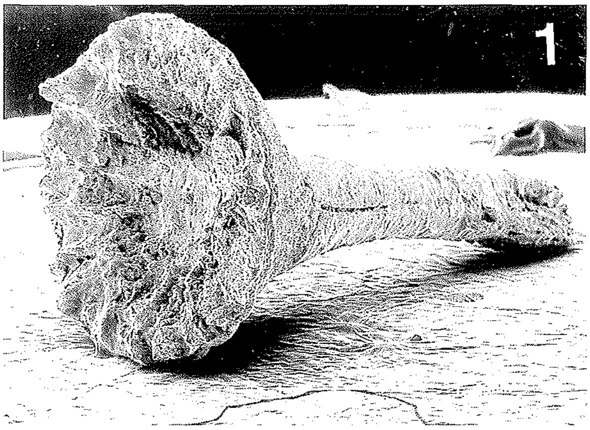


PLATE 3

Pyrgopolon (*Pyrgopolon*) *trochoides* (NYST, 1845)

1-3 – Same specimen as in Pl. 2, Fig. 1: 1 – Oblique top view, to show the right lateral groove; 2 – Top view of the cup; 3 – Close-up view of the peduncle/cup junction, to show the network of grooves
4 – MGPD 28721/1: top view of the cup
5-6 – Same specimen as in Pl. 2, Figs 2-6: 5 – Close-up view of the peduncle/cup junction, to show its surface when the outermost layer is peeled off; 6 – Base of the peduncle
7-8 – MGPD 28723/1: 7 – Oblique lateral view, 8 – Top view of the cup

All specimens from the Possagno Marl, Possagno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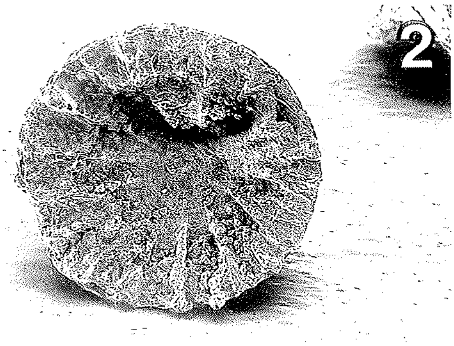
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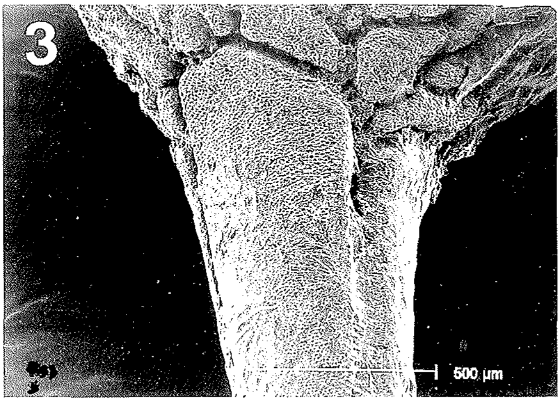
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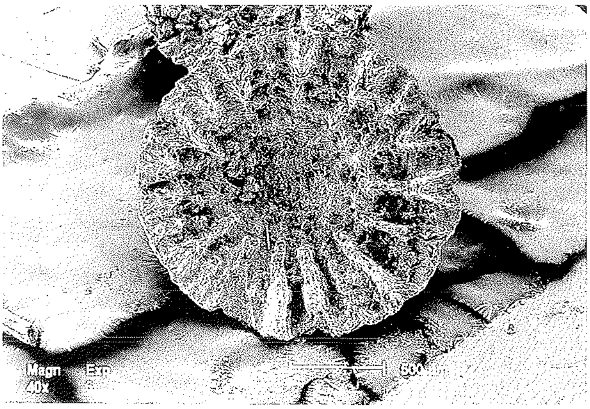
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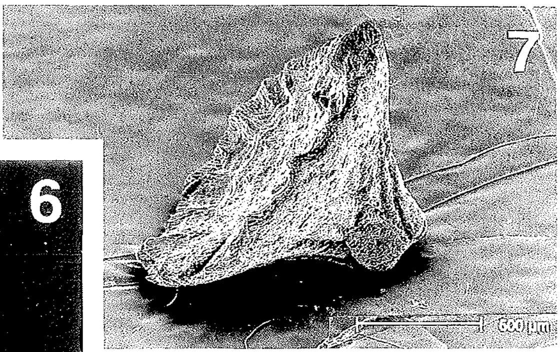
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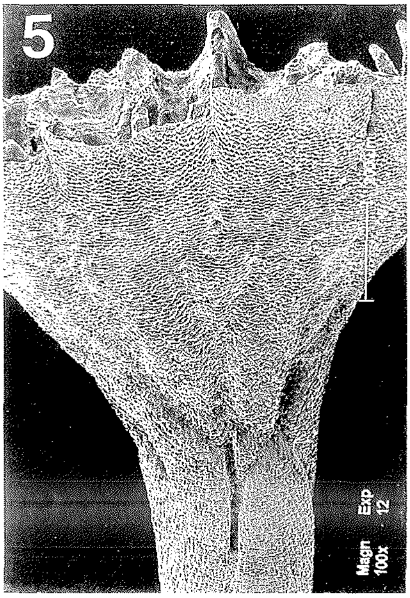
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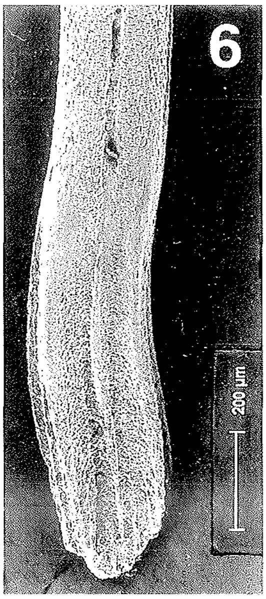
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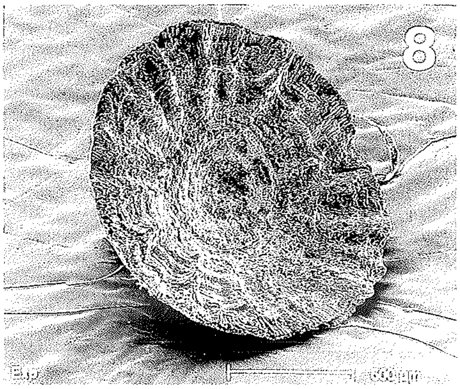
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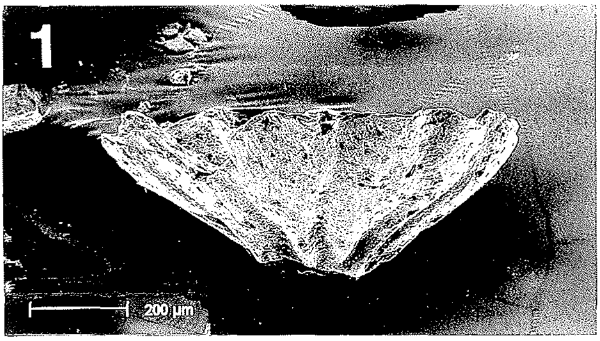
PLATE 4

Pyrgopolon (*Pyrgopolon*) *trochoides* (NYST, 1845)

1-2 – MGPD 28721/2: 1 – Lateral view of the cup, 2 – Top view of the cup
3-5 – MGPD 28721/3: 3 – Top view of the cup; 4 – Left lateral view (arrowed is a part magnified in Fig. 5); 5 – Close-up view of the cup margin, to show the structure when the outermost layer is peeled off
6-8 – MGPD 28721/4: 6 – Oblique lateral view, to show the outermost layer in position (arrow indicates part magnified in Fig. 8); 7 – Top view of the cup; 8 – Close-up view of the peduncle, partly exfoliated

All specimens from the Possagno Marl, Possagno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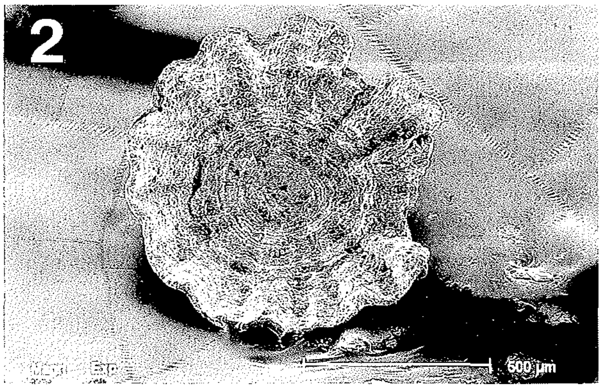
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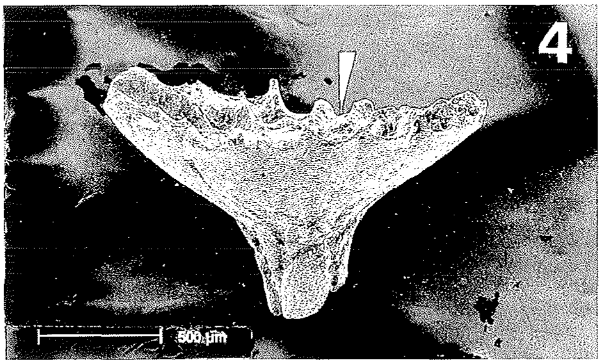
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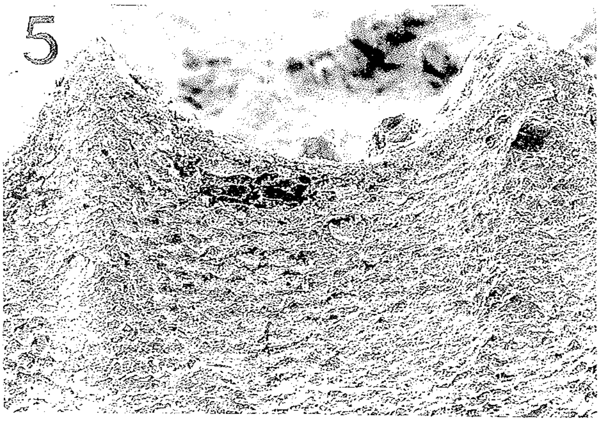
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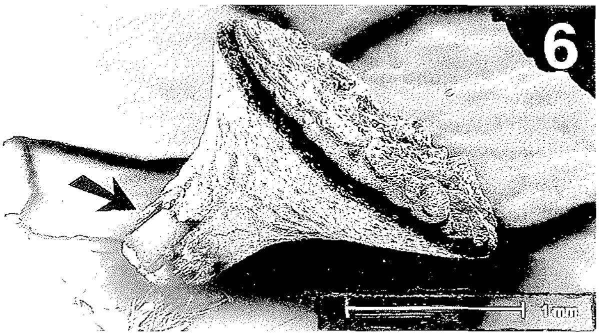
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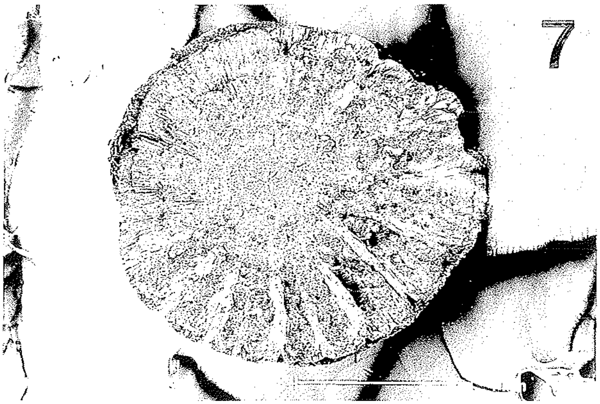
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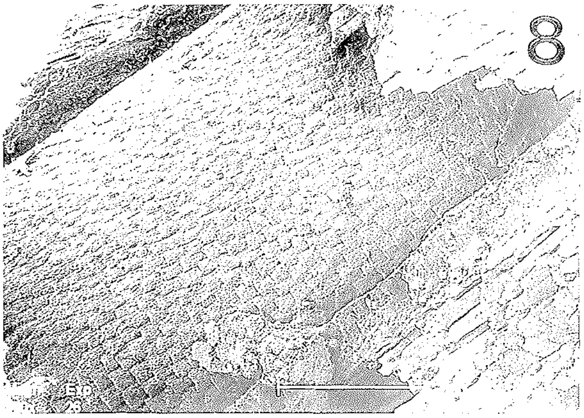
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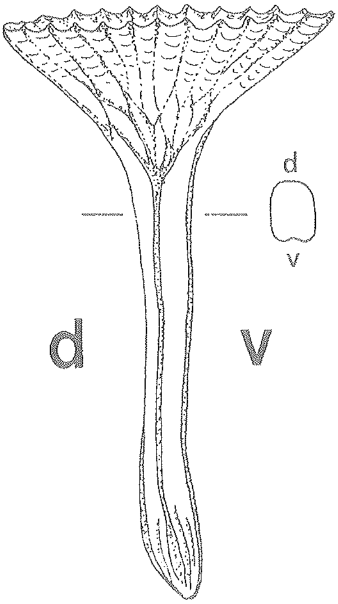
PLATE 5

Pyrgopolon (*Pyrgopolon*) sp.

Sketch-drawing shows the reconstruction of a complete operculum in right lateral view, and a cross-section of the peduncle: **d** – dorsal side, **v** – ventral side

1-6 – MGPD 28725/1: 1 – Top view of the cup; 2 – Left lateral view; 3 – Oblique outer view; 4 – Left lateral view; 5-6 – Close-up views, to show the ridges adorned with tubercles

The specimen from the Possagno Marl, Possagno



Pyrgopolon (*Pyrgopolon*) sp.

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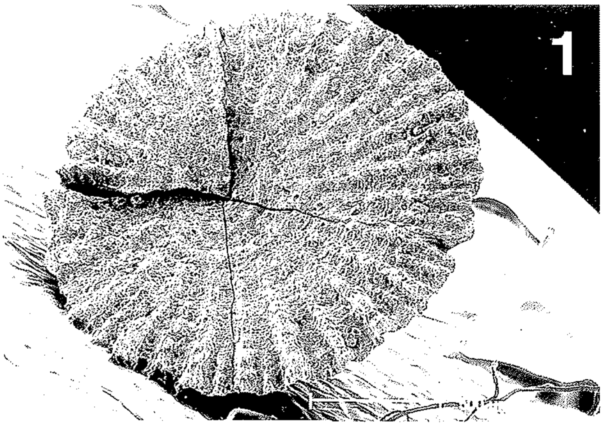

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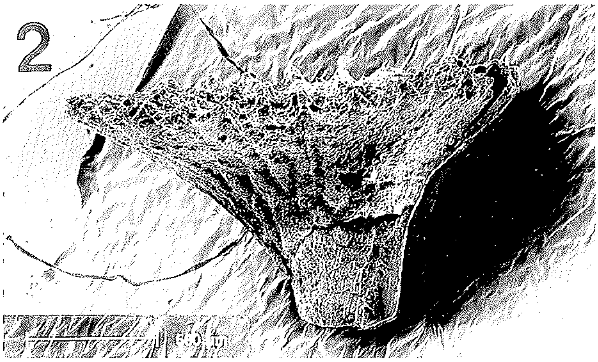

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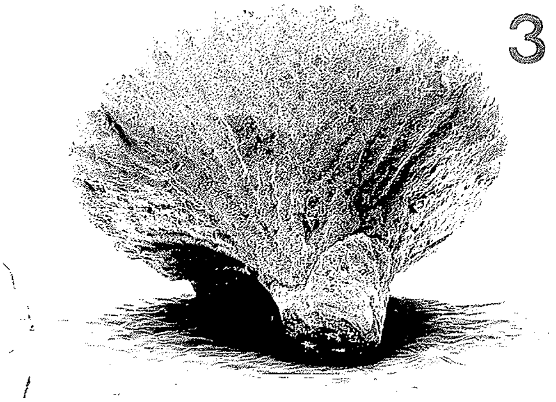

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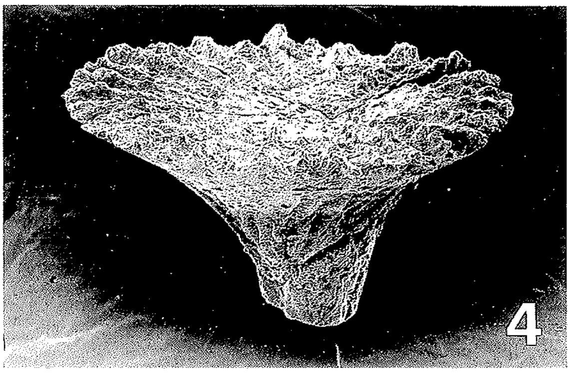

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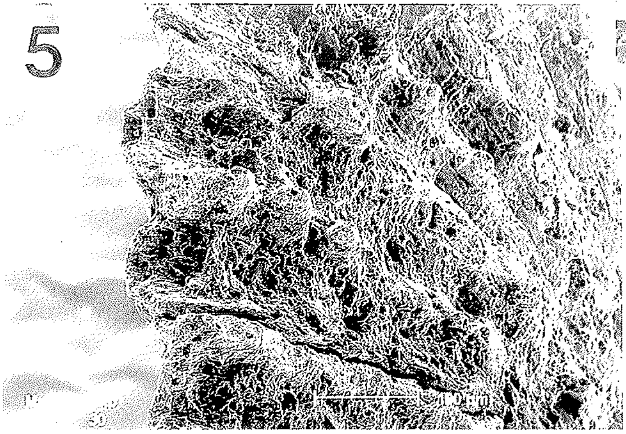

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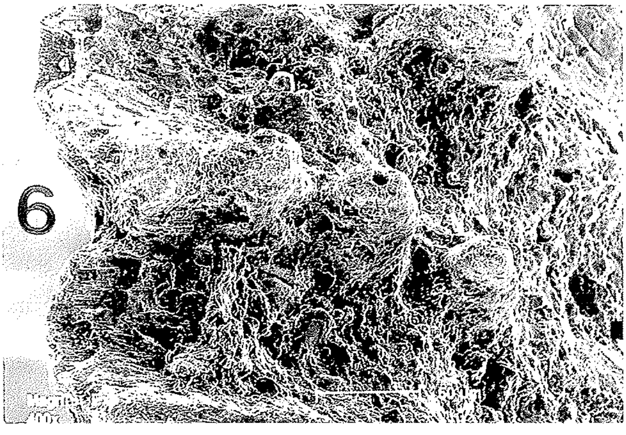
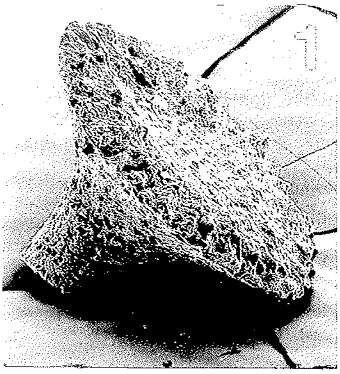


PLATE 6

Pyrgopolon (*Pyrgopolon*) sp.

1-3 – MGPD 28725/2: 1 – Oblique lateral view, 2 – Left lateral view, 3 – Top view of the cup
4-6 – MGPD 28725/3: 4 – Oblique lateral view; 5 – Top view of the cup (arrow indicates part magnified in Fig. 6); 6 – Close-up view, to show the structure of the ridges
7-9 – MGPD 28725/4: 7 – Oblique outer view, 8 – Oblique top view, 9 – Right lateral view

All specimens from the Possagno Marl, Possagno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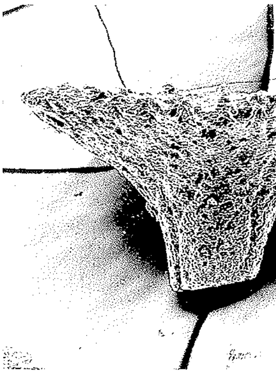

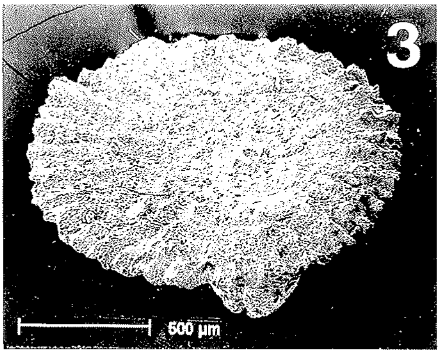
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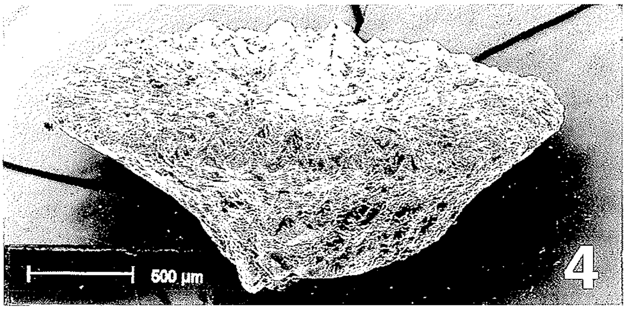
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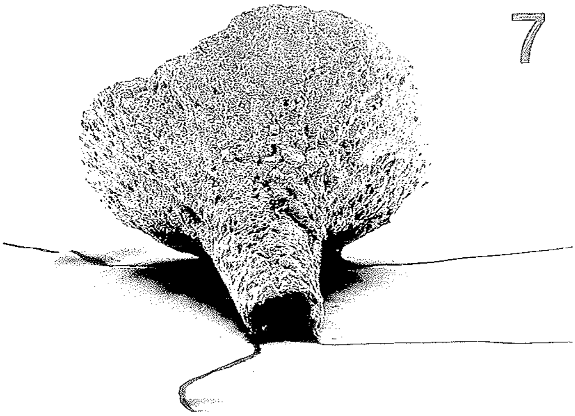
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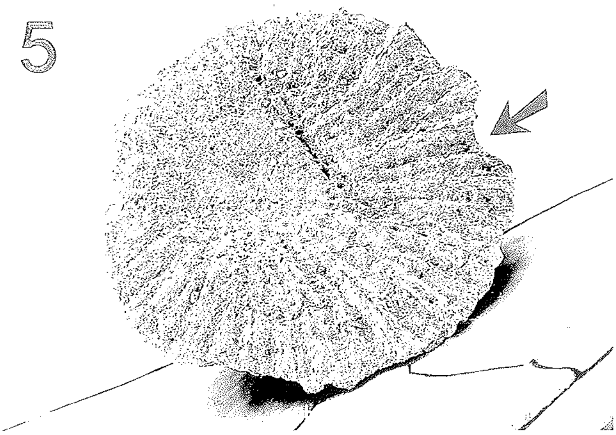
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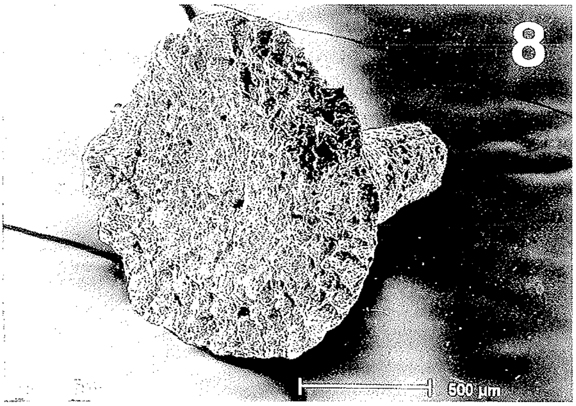
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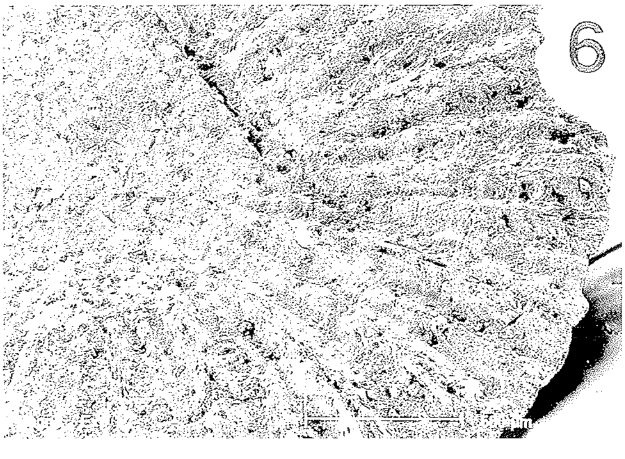
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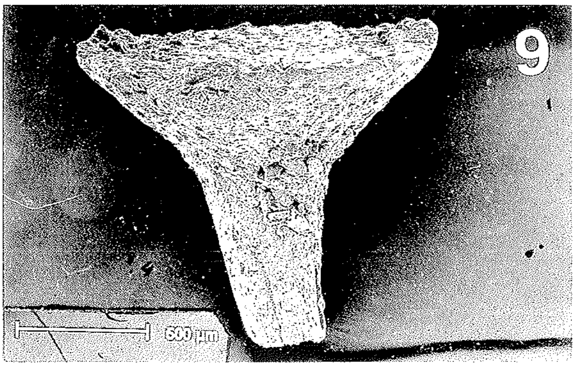
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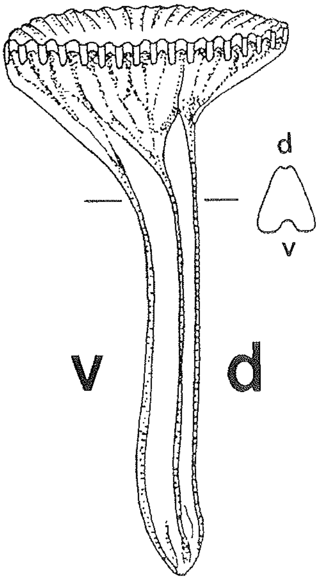
PLATE 7

Pyrgopolon (*Turbinia*?) *cunialense* sp.n.

Sketch-drawing shows the reconstruction of a complete operculum in left lateral view, and a cross-section of the peduncle: **v** – ventral side, **d** – dorsal side

1-3 – Holotype, MGPD 28726: 1 – Right lateral view; 2 – Top view of the cup; 3 – Oblique outer view, to show the outline of the peduncle in cross-section
4 – Paratype, MGPD 28727: Outer view of the cup
5-6 – Paratype, MGPD 28728: 5 – Left lateral view, 6 – Top view of the cup

All specimens from the Possagno Marl, Possagno



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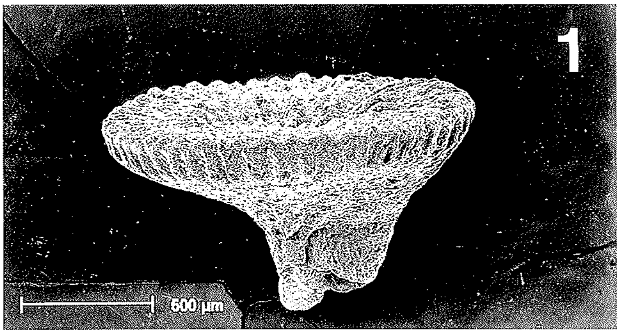

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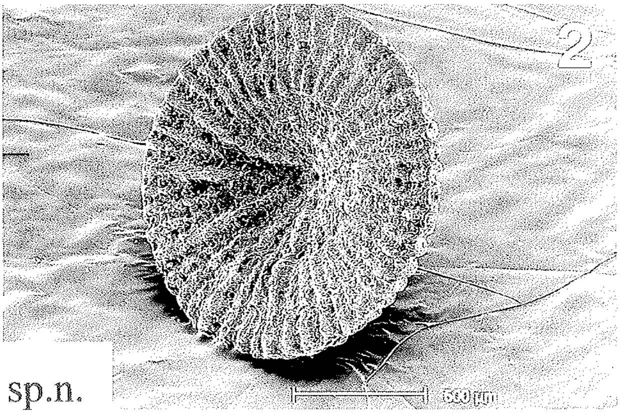

Pyrgopolon (*Turbinia*?) *cunialense* sp.n.

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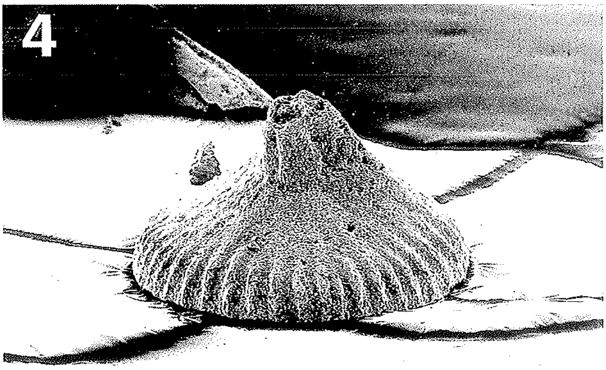

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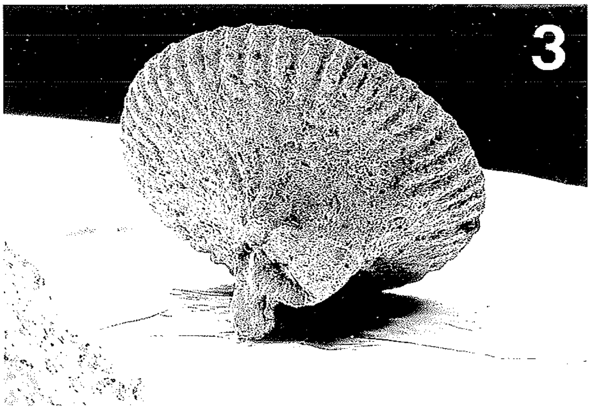

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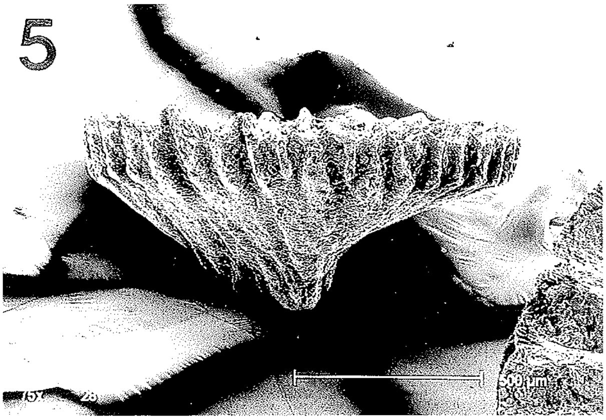

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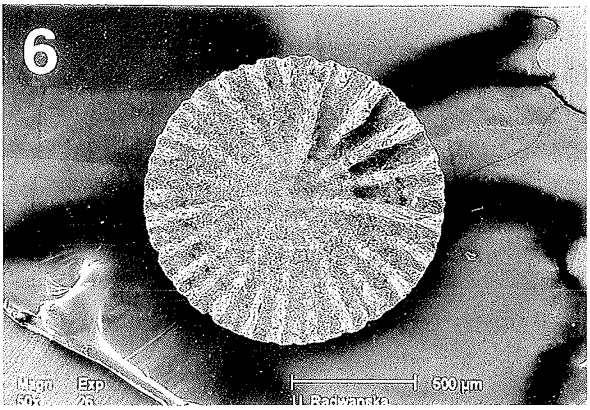
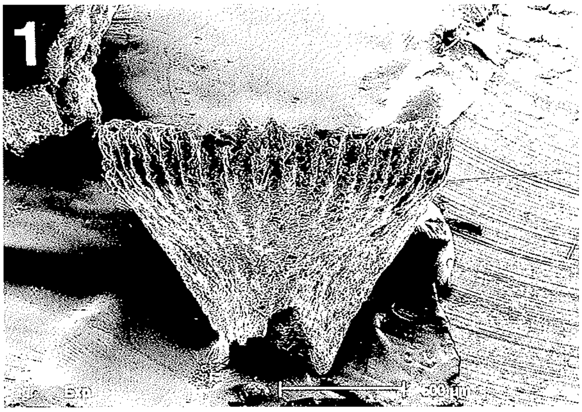


PLATE 8

Pyrgopolon (*Turbinia*?) *cunialense* sp.n.

1-3 – Paratype, MGPD 28729: 1 – Lateral view, 2 – Oblique top view, 3 – Top view of the cup
4-5 – Paratype, MGPD 28731: 4 – Top view of the cup, 5 – Right lateral view
6-7 – Paratype, MGPD 28732: 6 – Right lateral view, 7 – Top view of the cup
8-9 – Paratype, MGPD 28733: 8 – Ventral view, 9 – Top view of the cup
10 – Paratype, MGPD 27830: lateral view

All specimens from the Possagno Marl, Possagno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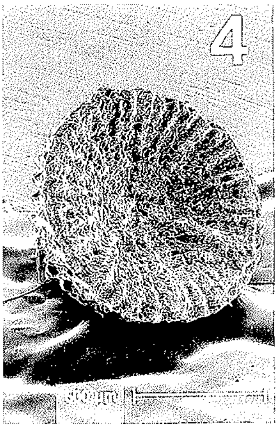
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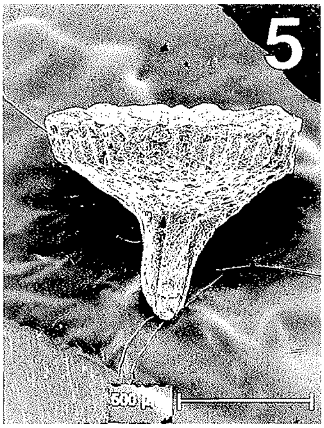
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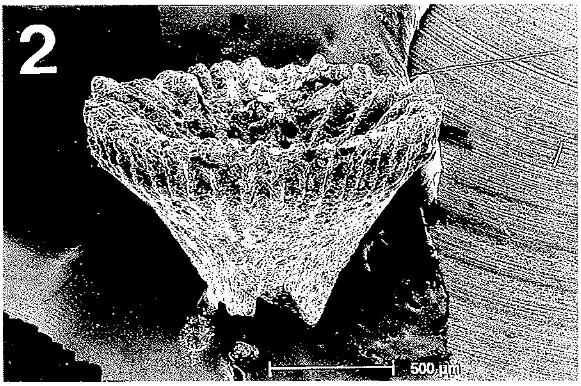
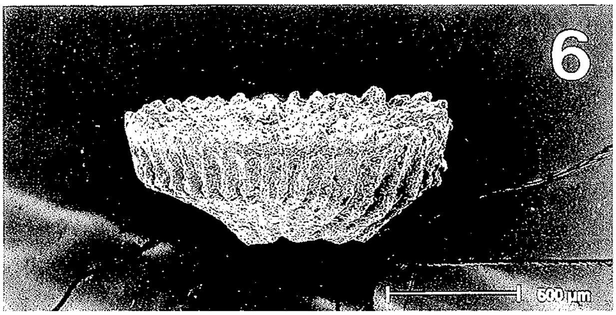
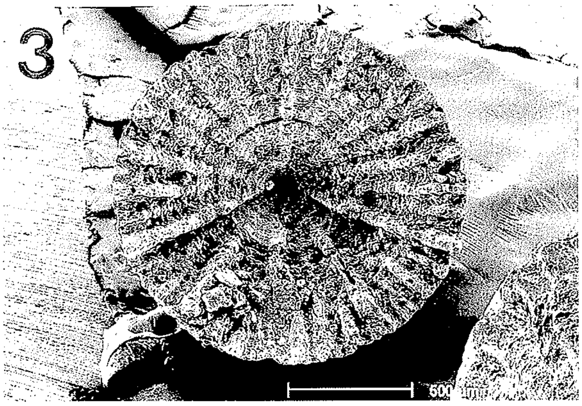
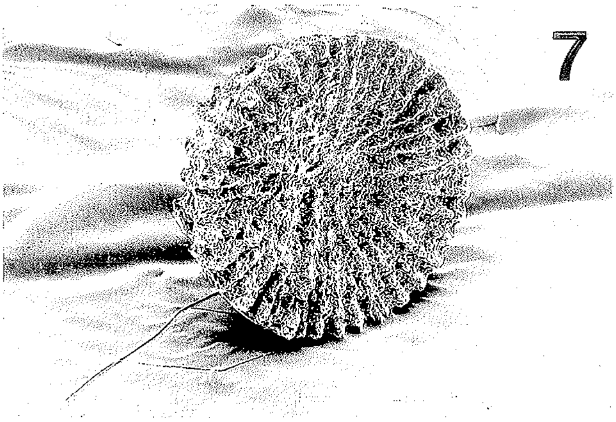
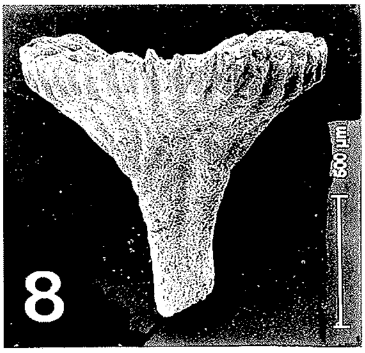
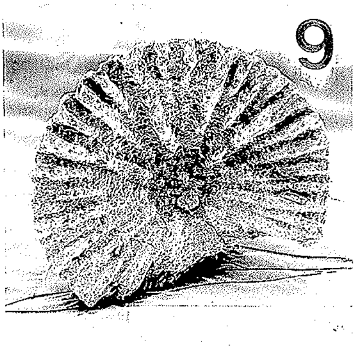

2
500 µm

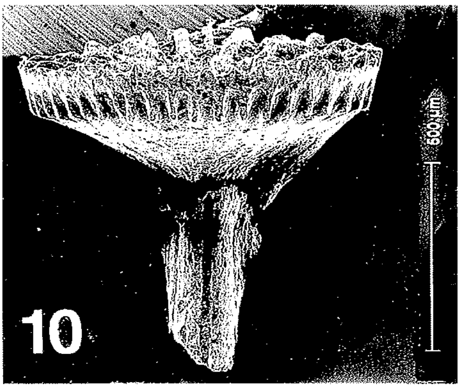

6
500 µm


3
500 µm


7


8
500 µm


9


10
500 µm