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Clavagellacea (Bivalvia) from the Tertiary of the Venetian region, NE Italy

ABSTRACT: The clavagellacean bivalves from the Tertiary of the Venetian region (NE Italy) are revised and some relevant morphological-descriptive terms are discussed, the term *crypt* being proposed to indicate the whole external construction of these tube-dwelling bivalves (burrow or borehole, calcareous lining, adventitious envelope, shell fused to the envelope). Two new species are described: *Clavagella (Stirpulina) veronensis* sp. n. from the Middle Eocene of the Verona province, and *C. (S.) vicentina* sp. n. from the Lower Oligocene of the Vicenza province.

INTRODUCTION

Representatives of the superfamily Clavagellacea usually are very rare. Although more than a hundred clavagellacean species (out of which some sixty probably valid) have been described, the general literature on this subject is scarce. It seems that only in three cases (Purchon 1956, 1960; Soliman 1971) the clavagellaceans were observed alive. The constructional morphology of this superfamily will be discussed in detail in a separate paper (Savazzi, *in preparation*). The aim of the present paper it to describe the clavagellaceans from the Tertiary of the Venetian region (NE Italy), and to provide a terminological framework for dealing with morphology of the structures produced by these peculiar bivalves.

Most clavagellaceans are tube-dwellers, *i. e.* bivalves enclosing themselves within an adventitious calcareous envelope embedded in soft sediments. The term *tube-dwelling* was used by Stanley (1970, p. 92) to describe the life habit of burrowing bivalves with cylindrical shells (e. g. *Ensis*). Subsequently, however, Carter (1978) used extensively this term in the sense given above. It seems reasonable to restrict the use of the term tube-dweling to bivalves building an adventitious cal-

careous envelope, since other forms can be adequately described as burrowers or burrow-dwellers.

Tube-dwelling forms occur in the Gastrochaenacea, Pholadacea, and Clavagellacea. In most cases, tube-dwellers are closely related to borers, and their adventitious envelope is clearly derived in phylogeny from the calcareous lining deposited by those primitive borers onto the walls of their borehole to consolidate the substrate and repair accidentally exposed borings. Sometimes, a single species can facultatively live as a borer or a tube-dweller. Therefore, the term *crypt* is here proposed to designate the whole external construction of tube-dwelling bivalves, which comprises the burrow or borehole, its lining, partial or total envelope, and the shell when fused to the envelope or cemented to the bored substrate.

This term has already been used in English literature to indicate the bivalve borehole. The term was derived from the common meaning of crypt as the cellar of a church. Its Greek etymology implies also the hiding and sheltering function. The extension of its meaning appears therefore legitimate.

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THE CLAVAGELLACEAN CRYPT

With few exceptions, the adult clavagellaceans live enclosed within a calcareous tubular crypt (Text-fig. 1). Some forms secondarily adapted to boring in solid substrates may have lost, at least in part, the capabilitv of building a complete envelope. In true tube-dwellers, the crypt is usually straight and long, with the shell lying near its anterior extremity. In *Penicillus* Bruguière, 1789, both the valves are fused to the envelope and visible externally. The adductor muscles are consequently absent or very reduced, but their muscle scars may persist. In *Clavagella* Lamarck, 1818, only the left valve is fused to the envelope, while the right one lies free within the envelope and articulates to the left. A flexible ligament is present, but the hinge is without any teeth. The genus *Humphreyia* Gray, 1858, represents an intermediate morphological state. Both its valves are united into a single calcareous plate, but the right one partly projects into the crypt. Nevertheless, there are reasons to believe that *Humphreyia* is not an evolutionary intermediate between *Clavagella* and *Penicillus* (see Smith 1962); it repre-

sents more likely a secondary adaptation to cementation. and is a Recent offshoot of *Clavagella*.

In all the tube-dwelling clavagellaceans the anterior part of the crypt carries a series of tubules or perforations. Purchon (1960) believed that water can be sucked into the crypt or expelled into the sediment through these openings, with the main purpose of embedding progressively the crypt into the sediment. The burrowing process appears, however, to be accomplished mainly by the outward-directed current (Savazzi, *in preparation*). The sucking of water from the surrounding sediment (usually a silty sand) is not effective in burrowing. However, it may be used by the animal to obtain additional food in form of suspended particles (Purchon 1960), or simply to inform it whether the anterior part of the crypt is completely buried.

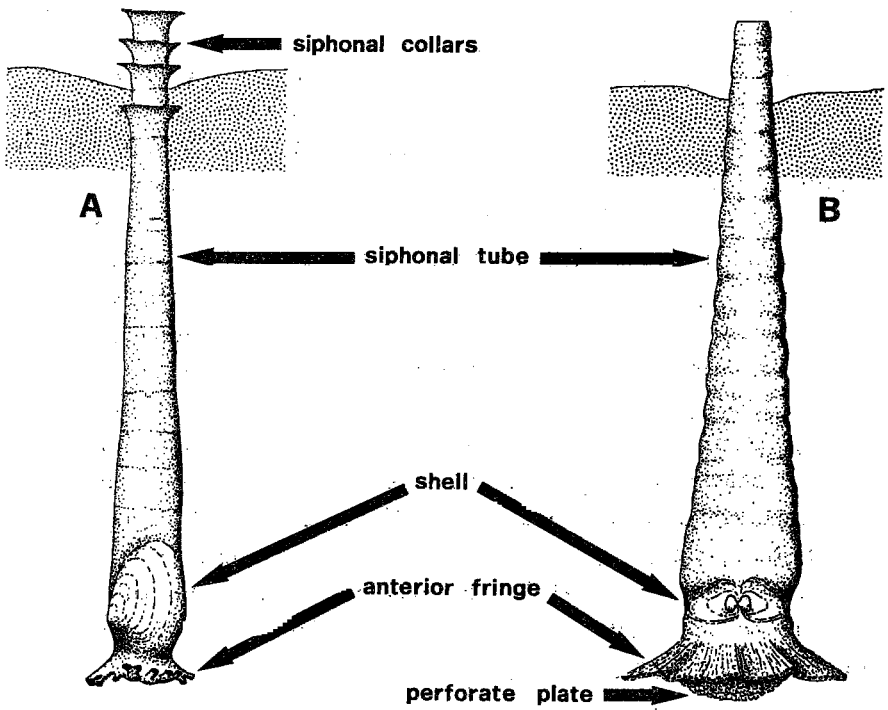

Fig. 1. Clavagellacean crypts in life position in soft sediments
A — *Clavagella (Stirpulina) coronata* Deshayes; Eocene, Paris Basin
B — *Penicillus (Penicillus) penis* (Linnaeus); Recent, tropical Indo-Pacific

The water pumping action is effected in *Penicillus* by movements of the highly muscular anterior part of the mantle. The small pedal opening in the mantle can close, acting as the valve of a piston pump.

These movements were actually observed by Purchon (1960). The genus *Clavagella* seems more primitive than *Penicillus*. Some of its Recent representatives might even be still primarily adapted to boring in solid substrates (Soliman 1971; Savazzi, *in preparation*). The anatomy of *Clavagella* is poorly understood. It is not certain whether it possesses a muscular mantle as found in *Penicillus*, but accessory ventral adductor muscles have been recorded. The main pumping action, however, is probably achieved by opening and closing the free valve against the other. In boring *Clavagella* the shell must be large, since the free valve is used to abrade mechanically the substrate. In the adult *Penicillus* the shell has no obvious function (Text-fig. 1*B*) and usually is very small. In burrowing *Clavagella*, to the contrary, the shell always fills up the anterior part of the crypt. Along with the presence of well developed adductor muscles this suggests that the free valve is functional, and one can hardly imagine any function different from water pumping in this case.

The anterior part of the crypt (except for the shell) usually does not show growth lines (Taylor & *al.* 1973). The few exceptions found (Savazzi, *in preparation*) do not invalidate the following interpretation. The lack of growth lines implies that this part, once built, is not subsequently modified. The most likely growth process is as follows: after a juvenile stage with articulated valves, which stage was actually recorded by Smith (1911) in *Humphreyia strangei*, the anterior part of the crypt is formed, including the anterior tubules. This predetermines the final adult size of the animal. While the anterior part of the crypt sinks progressively into the sediment due to the hydraulic burrowing mechanism, the siphonal processus grows up and its tip secretes a calcareous siphonal tube. The siphonal tube may account for more than 90% of the total length of the adult crypt. Once the adult length is attained, a series of collars or collar-like structures can be formed arround the distal extremity of the siphonal tube (Text-fig. 1*A*). Their apparent function is to prevent further sinking in the substrate (Savazzi, *in preparation*).

Most Recent and fossil clavagellaceans are typical of shallow-water marine habitats. Some can live (or at least survive) in intertidal environments, but this is certainly not their preferred environment. There is also a Recent species, *Clavagella multangularis* Tate, that occurs in deep waters. The earliest known forms, namely those from the Upper Cretaceous, are not substantially different from Recent *Clavagella*. Representatives of the superfamily are distributed all over the world, with a preference for temperate and warm seas.

SYSTEMATIC DESCRIPTION

Genus *CLAVAGELLA* Lamarck, 1818
Subgenus *STIRPULINA* Stoliczka, 1870
Clavagella (Stirpulina) veronensis sp. n.
(Text-fig. 2 and Pl. 1, Figs 1—6)

Holotype: Specimen figured in Pl. 1, Figs 1—6.
Type horizon: Middle Eocene.
Type locality: S. Maria di Negrar (Verona province).
Derivation of the name: After the town of Verona.

Diagnosis: Left valve long, moderately inflate; umbo subcentral slightly displaced towards anterior margin; adductor muscle scars near anterior and posterior margins; anterior adductor scar twice smaller than the posterior one; a single, anterior, rather irregular row of short tubules; pedal slit[1] closed; proximal part of siphonal tube cylindrical (distal unknown); outer surface of crypt, including proximal part of siphonal tube, agglutinated with sediment particles.
Material: A single specimen (housed at the Institute of Geology, Padova, No. *26124*).

Description. — The holotype is an internal mold of the anterior region of a crypt, preserved along with the left valve and a part of the siphonal tube. A small portion of the corresponding outer mold of the anterior part of the crypt with fringe tubules is also available.

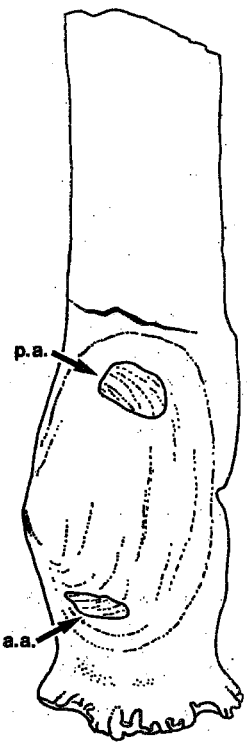

Fig. 2
Clavagella (Stirpulina) veronensis sp. n.
Middle Eocene, S. Maria di Negrar (Verona province, NE Italy); ×2
a.a. and *p.a.* anterior and posterior adductor muscle scars, respectively

[1] Pedal slit is a structure in the anterior part of the crypt, facing the pedal opening in the mantle.

The hinge of the left valve projects inside the crypt. The inner surface of the envelope is folded, forming projecting ridges. These ridges are indicative of the morphogenetic process producing the anterior part of the crypt (Savazzi, *in preparation*).

The length of the siphonal tube and its distal extremity are unknown. Supposedly, the tube was several centimeters long.

An artificial cast has been made from the outer mold (Pl. 1, Fig. 5). Its rough surface is more likely due to the material agglutinated at the outer surface of the crypt, than to an artifact of preservation. The anterior tubules, however, are not agglutinated.

Remarks. — Comparisons with congeneric species can be done mainly after the shell outline and proportions, since the internal characters are generally unknown.

Most representatives of the genus *Clavagella* have much shorter valves than *C. veronensis* sp. n., while those species with shells similar in size have the umbo located much nearer the anterior shell margin (e.g. *C. caillati* and *C. coronata* from the Eocene of France). The presence of anterior tubules in form of a rather well delimited fringe (*corona* of Smith 1962, Keen & Smith 1969) justifies the assignment of the investigated species to the subgenus *Stirpulina*, in which the end of the siphonal tube carries a series of sharp collars.

Clavagella (Stirpulina) vicentina sp. n.
(Text-fig. 3 and Pl. 2, Figs 1—8)

1973. *Teredo* sp.; Coletti, Piccoli, Sambugar & Vendemiati dei Medici [*partim*], Pl. 3, Fig. 1.

Holotype: Specimen figured in Pl. 2, Figs 1—4 (Coll. No. *10460*).
Paratype: Specimen figured in Pl. 2, Figs 5—8 (Coll. No. *10459*).
Type horizon: Lower Oligocene.
Type locality: Trappolino di Cereda (Vincenza province).
Derivation of the name: After the town of Vincenza.

Diagnosis: Left valve moderately long and inflate, obliquely truncated in postero-ventral region; umbo subcentral; anterior fringe supposedly composed of a single row of short tubules; proximal part of siphonal tube cylindrical (distal part unknown); outer surface of crypt smooth, not agglutinated.
Material: Two specimens (housed at the Institute of Geology, Padova, Nos *10459—10460*).

Description. — The investigated specimens represent the anterior region of two crypts, each with a part of the siphonal tube, the holotype also with the fringe tubules partly preserved.

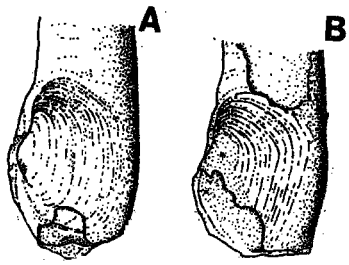

Fig. 3
Clavagella (Stirpulina) vicentina sp. n.
Lower Oligocene, Trappolino di Cereda (Vicenza province, NE Italy); nat. size
A — holotype, **B** — paratype

The specimens resemble in morphology *C. veronensis* sp. n. However, they show a shorter postero-ventrally truncated shell with smooth outer surface. Somewhat irregular folds occur at the crypt wall opposite to the left valve.

Remarks. — The holotype of *C. vicentina* sp. n. was first illustrated by Colleti & *al.* (1973) as *Teredo* sp., together with a true teredinid tube stored along with it. Two other calcareous tubes, one of which may be the siphonal extremity of a clavagellacean crypt with projecting fringes, are also stored with this material.

Clavagella (Stirpulina) cf. *oblita* Michelotti, 1861
(Text-fig. 4)

1861. *Clavagella oblita* n. sp.; Michelotti, p. 53, Pl. 5, Figs 8—9.
1962. *Clavagella (Stirpulina) oblita* Michelotti; Smith, p. 170.

Material: One specimen (housed at the Institute of Geology, Padova, No. *26126*).

Description. — The investigated specimen presents the anterior part of a crypt preserved along with both the valves but without tubules. The valves are oblique, almost equally high as long.

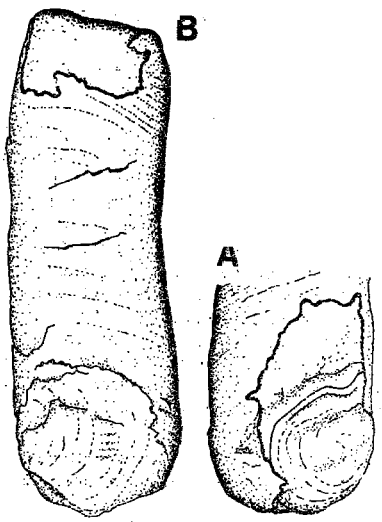

Fig. 4
Clavagella (Stirpulina) cf. *oblita* Michelotti
Upper Eocene, Costalunga near Possagno (Treviso province, NE Italy); ×2
A — right valve, **B** — crypt along with left valve

Remarks. — The investigated specimen cannot be unequivocally separated from, or assigned to, *Clavagella oblita* Michelotti because the latter species has been insufficiently illustrated. Its valves resemble also in outline the species *C. bacillum* (Brocchi) as illustrated in the present paper (Pl. 1, Fig. 10).

Occurrence. — The investigated specimen was found in the Upper Eocene of Costalunga near Possagno (Treviso province).

The species *Clavagella oblita* has been recorded in the Oligocene of NW Italy (Michelotti 1861), Hungary and Egypt (Smith 1962).

Clavagella sp.
(Pl. 1, Figs 7—9)

Material: A single fragmentary specimen (housed at the Institute of Geology, Padova, No. *26125*).

Description. — The specimen represents the anterior part of a crypt preserved along with traces of the left valve, recovered from a boring in the beach-rock

pebble. A large myophore-like structure seems to project inside the crypt from the cardinal region of the left valve. The left valve seems to have been narrow and oblique, rhomboidal in outline.

Remarks. — Myophore-like processes, although somewhat differently developed, have already been recorded in the clavagellaceans (Carter 1978).

Occurrence. — Oligocene of Cavalo (Verona province).

"Clavagella" dalpiazi Venzo, 1941

1941. *Clavagella dalpiazi* n. sp.; Venzo, pp. 185—186, Pl. 1, Figs 12*a*—*b* and 13.

Remarks. — This is the only clavagellacean bivalve recorded previously from the Venetian region, at least at the species level. The original illustrations given by Venzo (1941) have been published with inverted sides. The author was aware of the error and noted it in a footnote to the caption. The species was described on the basis of the two illustrated specimens, without designating the holotype. The indication of the repository was incomplete due to a typing error. Probably, it was intended to be "Museo Trento". The paleontological collections of the Natural History Museum at Trento, however, are awaiting reordering, and an extensive search for this material has turned out to be unsuccessful (G. Tomasi, *pers. communication*). Possibly, the material has been lost during the last war.

It is apparent from the description as well as from the illustrations that both the valves are enclosed within the envelope. This indicates clearly that the considered form cannot be representative of *Clavagella*. The species *Clavagella cornigera* Schafhäutl, 1863, from the Upper Cretaceous of Bavaria was described by Smith (1962) as possibly having both the valves free, but this may well be an artifact of preservation. The Clavagellacea most probably evolved from some deep-burrowing Pandoracea or Poromyacea (*see* Smith 1962, Carter 1978). Tube-dwelling forms are not likely to have evolved from those burrowers through some unknown "preclavagellids" with both valves free in the crypt, but rather through blocarbonate borers using the cemented valve as a pivot for abrading mechanically the substrate with use of the other valve (Soliman 1971; Savazzi, *in preparation*). The assignment of the considered form to the Clavagellacea is furthermore counterevidenced by the presence of transversal growth lines on the anterior part of the envelope. These growth lines, the antero-ventral pedal gape, and the pear-shaped crypt are indicative of an affinity to the Gastrochaenacea. As a matter of fact, the anterior part of the crypt is periodically bored and resecreted in the Gastrochaenacea in order to permit further growth (hence, the growth lines), and the shell is free to move forward into the newly built bottom of the crypt.

The species *dalpiazi* Venzo is therefore to be excluded from the Clavagellacea. Its proper systematic position, however, can be established only after reexamination of the type material.

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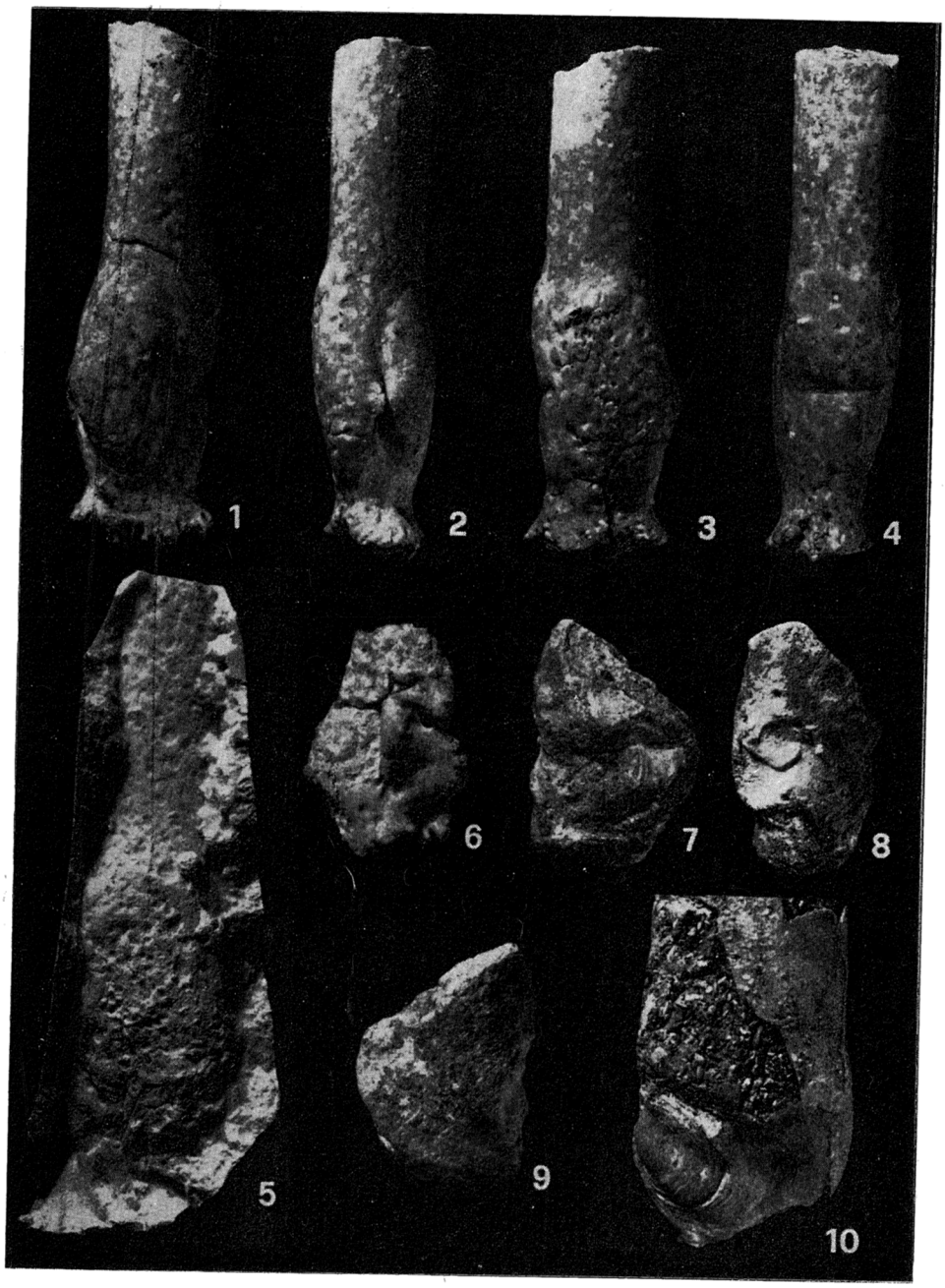
MAŁŻE Z NADRODZINY CLAVAGELLACEA Z TRZECIORZĘDU OKOLIC WENECJI

(Streszczenie)

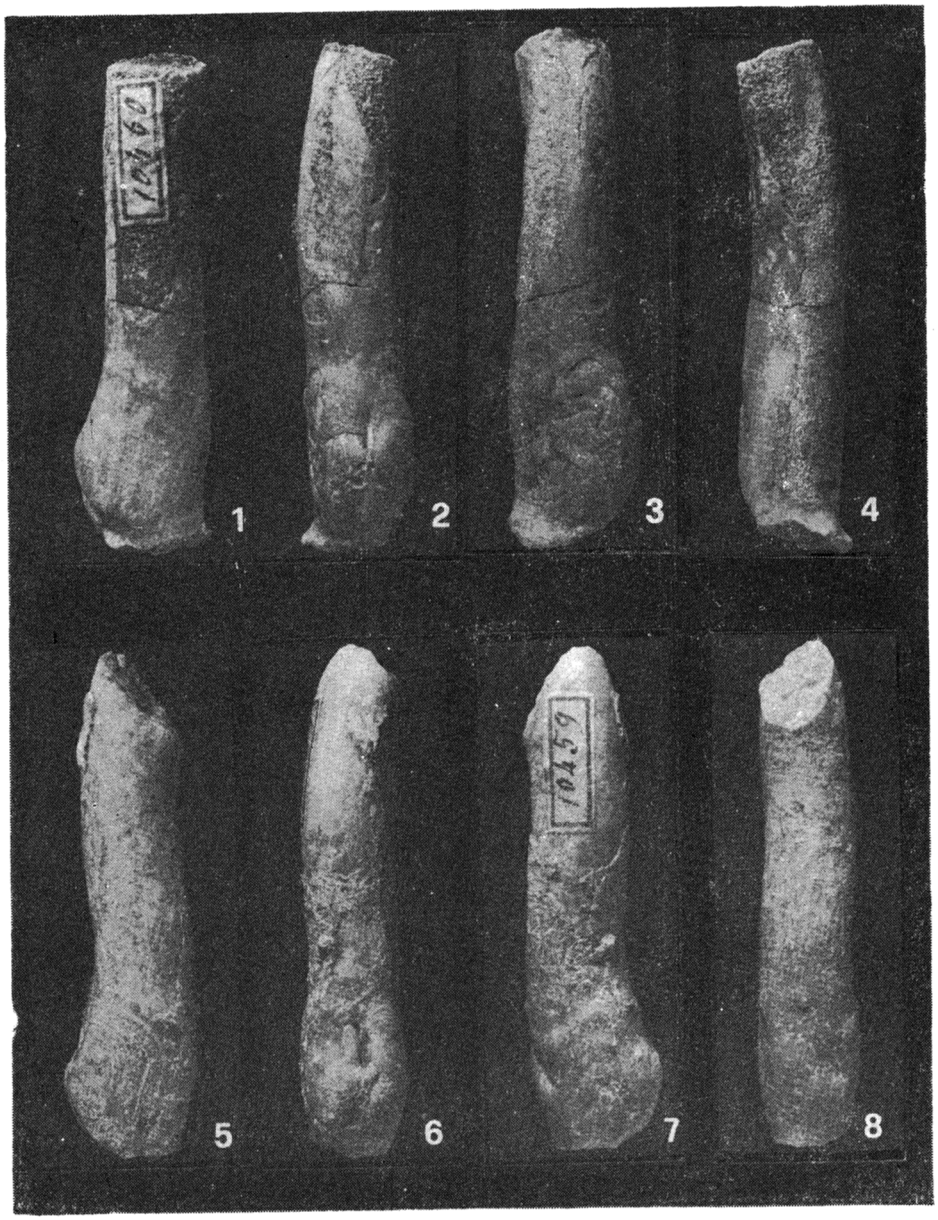
Przedmiotem pracy jest rewizja małży z nadrodziny Clavagellacea występujących w utworach trzeciorzędu okolic Wenecji we Włoszech. Analiza starszych kolekcji oraz nowego materiału, a także badania porównawcze dzisiejszych przedstawicieli nadrodziny Clavagellacea pozwoliły na dokładniejsze studia ekologiczne nad tymi aberantnymi małżami, wytwarzającymi rurkowatą osłonę syfonów dla zabezpieczenia przed pogrzęzaniem organizmu w miękki osad (*patrz* fig. 1). W części systematycznej pracy (*patrz* fig. 2—4 oraz pl. 1—2) opisano m.in. dwa gatunki dla nauki nowe: *Clavagella (Stirpulina) veronensis* sp. n., oraz *Clavagella (Stirpulina) vicentina* sp. n.



1—6 — *Clavagella (Stirpulina) veronensis* sp. n. (*holotype*); Middle Eocene, S. Maria di Negrar (Verona province, NE Italy)
1—4 inner mold, ×1.5; *5* artificial cast of outer mold, with agglutinated outer surface, ×1.5; *6* anterior view of inner mold, with pedal slit at the center, ×2

7—9 — *Clavagella* sp.; Oligocene, Cavalo (Verona province, NE Italy); ×1.5
7 left, *8* dorsal, and *9* right views of the anterior part of crypt

10 — *Clavagella (Stirpulina) bacillum* (Brocchi); Pliocene, Castell'Arquato (Piacenza province, NW Italy); anterior part of crypt preserved along with the left valve; ×2



1—8 — *Clavagella (Stirpulina) vicentina* sp. n.; Lower Oligocene, Trappolino di Ceredo (Vicenza province, NE Italy); ×1.5
1—4 holotype (left, dorsal, right, and ventral views of crypt, respectively), *5—8* paratype (left, dorsal, right, and ventral views of crypt, respectively)