Contr. Tert. Quatern. Geol. 30(3-4) | 155-175 7 figs, 1 tab, 3 pls. Leiden, December 1993

# *KUPHUS MELITENSIS*, A NEW TEREDINID BIVALVE FROM THE LATE OLIGOCENE LOWER CORALLINE LIMESTONE OF MALTA

GEORGE ZAMMIT MAEMPEL
Birkirkara, Republic of Malta

Zammit Maempel, George. *Kuphus melitensis*, a new teredinid bivalve from the Late Oligocene Lower Coralline Limestone of Malta. — Contr. Tert. Quatern. Geol., 30(3-4): 155-175, 7 figs, 1 tab., 3 pls. Leiden, December 1993.

A new species of teredinid bivalve, *Kuphus melitensis*, is described on the basis of valves, tubes and pallets from the marine Lower Coralline Limestone Formation (Late Oligocene) of Malta (central Mediterranean). The valves are preserved as moulds, the pallets as stalks without an awn. This is the first fossil record of valves and pallets of the genus *Kuphus* Guettard, 1770. The hard part morphology of the new species is compared with that of its Recent congener, *Kuphus arenarius* (Linné, 1758). The abundant fossil tube material available has provided not only a documentation of such features as shell impressions, localised swellings, calcareous encrustations, bifurcation, repair, periodic angulation, internal cameration, anterior and internal closure of tubes, but also clarification of the stages of development of its calcareous siphonal tubes. These unique tube features are described and interpreted in the light of the animal's ability to deposit and resorb calcium carbonate. As all previous fossil *Kuphus* records are based solely on tubes, they are essentially indeterminate Teredinidae, and only Maltese material is positively identified to species level. From an almost world-wide distribution in tropical and temperate Cainozoic shallow seas, *Kuphus* is now restricted chiefly to the brackish waters and mangrove swamps of the Indo-Pacific region.

Key words — Bivalvia, Teredinidae, Late Oligocene, Malta, new species, hard part morphology.

G. Zammit Maempel, MQR, D.Sc. (honoris causa), MD, 53 Main Street, Birkirkara, Malta BKR 05.

## Contents



## Riassunto

Dal 'Lower Coralline Limestone' — una formazione del Oligocene Superiore dell'isola centro mediterranea di Malta — si segnala *Kuphus melitensis*, una nuova specie di mollusco bivalva appartenente alla famiglia dei Teredinidae. Questa é anche la prima segnalazione delle valvole e delle palette del genere *Kuphus* nello stato fossile. La morfologia delle parti duri del mollusco terziario maltese é qui comparata a quella del analogo vivente, *Kuphus arenarius* Linné. L'abbondante materiale di tubi di *Kuphus melitensis* ha proveduto, non soltanto documentazione delle varie chiusure interne ed esterne del tubo, dei fori associati colle chiusure esterne, delle gonfiature associate con alcune di quelle interne, di impressioni sul guscio di fossili adiacenti e di encrostazioni organiche, ma anche evidenze che chiariscono i varii stadi di sviluppo dei tubi siphonali calcarei. Tutte le precedenti segnalazioni specifiche di *Kuphus* fossile sono basate soltanto sulle dimensioni e forme dei tubi — criteri non abbastanza validi. Di conseguenza, si considerano questi come Teredinidae o *Kuphus* indeterminabili e si considera positivamente identificabile al livello specifico soltanto il materiale Maltese basato su valvole, palette e tubi. Da una distribuzione quasi mondiale nei bassifondi tropicali e temperate durante l'epoca terziaria, il genere *Kuphus* e presentemente ristretto, quasi unicamente, alle aque salmastre e ai 'Mangrove swamps' della regione Indo-Pacifica.

## Introduction

Hitherto, all fossil records of the teredinid bivalve *Kuphus* have been of the calcareous tubes only. Described in the present paper are not only the tubes of fossil *Kuphus*, but also its valves and pallets, found for the first time in the fossil state and in association with the calcareous tubes. In Malta, such tubes penetrate the limestone strata more or less vertical as in life (Pl. 1, Fig. 1) but may occasionally be inclined 30-40° to the vertical. In places, there has been a certain amount of destruction and reworking of the fragmented tubes into the horizontal position during Oligo-Miocene times. Except for a few isolated derived tube fragments, they are almost always encountered in very large numbers or colonies, forming horizontal beds, 50-150 cm thick, herein referred to as '*Kuphus* Beds.' These units are limited to the Lower Coralline Limestone Formation (Chattian, Late Oligocene) and occur throughout its whole extent. The associated fauna indicates a marine environment.

The '*Magilus grandis* horizon' described by Tornquist (1904) and by Cottreau & Collignon (1924) as occurring in Burdigalian (Miocene) deposits on the 'Ile de Mokamby' (SW Africa) and in Madagascar, the so-called '*Vermetus* Beds' in the Burdigalian Asmari Limestone of Iran (Douglas, 1927) and the 'Beds of *Kuphus*' reported by Cottreau (1912) from the Miocene of the Mediterranean coast of France (Sousset area, Bouche du Rhône), are all analogous to the Maltese '*Kuphus* Beds'. Fossil *Kuphus* tubes are known mainly from the Miocene of the Caribbean (Gabb, 1873, 1881; Maury, 1925; Oostingh, 1925; Rutsch, 1942; Jung, 1971), France (Cottreau, 1912), Zanzibar (Cox, 1927), Iran (Douglas, 1927; Cox, 1927), Sri Lanka (Deraniyagala, 1969) and the Oligocene beds of Malta (Spratt, 1852; Jones, 1866; Adams, 1870; Oppenheim, 1916; Felix, 1973; Zammit Maempel, 1977, 1979, 1982; Bosence *et al.*, 1980; Geys & Beeusaert, 1982; Pedley *et al.*, 1990).

Sufficient material has been recovered to allow the clarification of the stages of development of the calcareous siphonal tubes in fossil *Kuphus* and to demonstrate its various internal and external features, including pallets, valves, internal and anterior closures, pittings, swellings, shell impressions and overgrowth of encrusting organisms. In Teredinidae the classification of the genera is based on the morphology of the soft parts and pallets (Turner, 1969, pp. N722, 723). The genus *Kuphus* is recognised by the characteristic bifurcated, long, siphonal end of the tube. In addition, other Teredinidae are obligate wood borers, but *Kuphus* is known to burrow only in muddy or sandy substrates.

Specific identification in teredinids is based on joint features of tubes, pallets and valves. As all fossil *Kuphus* 'species' recorded hitherto in the literature are based solely on the size and shape of tube fragments, their validity is doubted and only Maltese material is identified positively to species level. Recorded species include:

— *Kuphus incrassatus* Gabb, 1873 (p. 246; see also Gabb, 1881, p. 342, pl. 44, fig. 12a-e), from the earthy shales of Guayabin (Santo Domingo), 'Middle Miocene', now thought to be Late Miocene.
— *Teredo (Cuphus) primigenia* Cossmann, 1921 (p. 13, pl. 11, fig. 21) from the 'Stampien' (Oligocene) of Cerens (France).
— *Cuphus arenarius* Linnaeus of Cottreau & Collignon (1924, pp. 278, 279) from the Burdigalian of Sousset (French Mediterranean coast).
— *Teredo (Kuphus)* aff. *polythalamia* (L.) of Cox (1927, pp. 62-64, pl. 8, fig. 1) from the Miocene of Pemba (Zanzibar Protectorate). These tubes are very similar to those of *Kuphus melitensis*.
— *Kuphus arenarius* (Linnaeus) of Douglas (1927) from the Miocene (Asmari Limestone) of Iran. These specimens too are very similar to Maltese material.
— *Kuphus ?arenarius ?lankae* Deraniyagala, 1969 (pp. 39-41) from the Late Oligocene or Early Miocene of Sri Lanka. This may be a misidentification, as the tubes are described as widening upwards and as occurring always in pairs.
— *Kuphus polythalamia* (Linné) of Jung (1971, p. 161) from the tuffaceous facies of the Grand Bay Formation (early Middle Miocene) of Curaçao (West Indies). The specimens I examined at the Naturhistorisches Museum, Basel, are smaller and much more delicate than *K. melitensis*.

## Distribution and stratigraphy

There is no previous detailed work on the Maltese Cainozoic *Kuphus* and the first publication to illustrate these tubes and the strata in which they occur is by Zammit Maempel (1977, p. 22, pl. 15). In the Maltese Islands, *Kuphus* tubes are restricted to the Attard Member of the Lower Coralline Limestone Formation (Fig. 2), which is now considered to be of Late Oligocene (Chattian) (Giannelli & Salvatorini, 1972; Felix, 1973) rather than Eocene (Forbes *in* Spratt, 1854) or Early Miocene age (Spratt, 1852, 1854). Local stratigraphy is summarised in Fig. 2 and localities yielding the fossil tubes are shown in Fig. 1.

In Malta, *Kuphus*-bearing beds are best seen at Wied Incita, Attard (central Malta) and San Pawl tat-Targa (along the Great Fault) where limestone quarry workers refer to the tubes as sigarri (cigars), terha (sash, band) or sallur (eels), depending on size and shape of the tubes (Zammit Maempel, 1989, pl. 2). Other exposures have been recorded in the Mar-

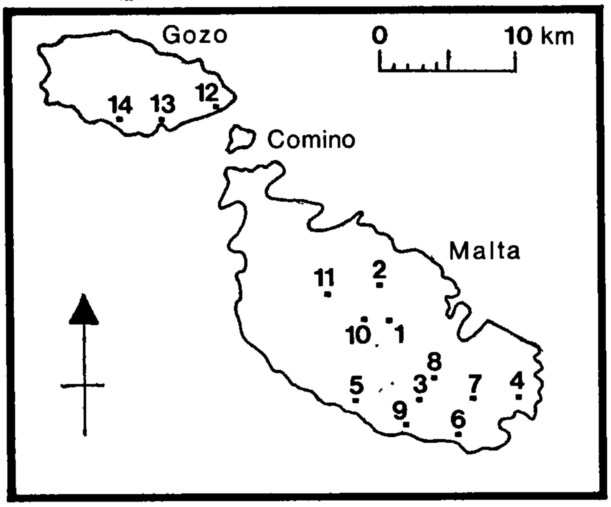



Fig. 1. Outline map of the Maltese Islands showing recorded *Kuphus* sites, 1 - Wied Incita, Attard; 2 - San Pawl tat-Targa; 3 - Maqluba, Qrendi; 4 - Marsaxlokk; 5 - Migra Ilma, Fawwara; 6 - Hal Far; 7 - Has Saptan; 8 - Ta' Kandja Water Galleries; 9 - L-Ilsna, Maghlaq (in alluvial Pleistocene deposit overlying downthrown Upper Coralline Limestone Formation); 10 - Ta' Qali Pumping Station; 11 - Mosta; 12 - Hondoq ir-Rummien; 13 - Mgarr-x-Xini; 14 - Ta' Cenc.

saxlokk area (Jones, 1866, p. 152), on the sides of the Maqluba subsidence structure, limits of Qrendi (Adams, 1870, p. 270, footnote 19) and Migra Ilma, SE Dingli, limits of Fawwara (Felix, 1973, p. 19). 'A horizon rich in tubes, lying 24-27 m below the base of the Globigerina Limestone', was encountered by T.O. Morris (pers. comm., 1973) when striking a shaft at Ta' Qali Pumping Station, central Malta. Its location is only two kilometres from the Wied Incita quarries and probably represents the extension of the *Kuphus* Beds in that area. In addition, the author has encountered isolated specimens in Cainozoic rocks at Mosta, Hal Far, Has-Saptan, Ta' Kandja water galleries and (reworked) in the Quaternary alluvial deposit at l-Ilsna, Maghlaq. In the nearby island of Gozo, the author could not locate any tubes in the Mgarr ix-Xini gorge where Adams (1870, p. 271, footnote 19) encountered them 'in large numbers', and only isolated specimens were found at Ta' Cenc and at Hondoq ir-Rummien.

All the above-mentioned sites have been visited by the author but only the exposures at the Wied Incita quarries have been studied in detail. The receding working face of this quarry complex was repeatedly investigated during the period 1964-79. It was from this site that all the specimens described and figured in this paper were collected.

*Kuphus* Beds vary in thickness at different localities in the Maltese Islands, but at Wied Incita (Fig. 3), where the bed is about 23 m below surface level, it is 90-150 cm thick. It is traceable over the faces of the adjoining quarries for a distance of several hundred metres as a soft, rubbly, rust-stained horizontal band wedged between white limestone of much greater hardness. In places, the bed is faulted several metres.

## Systematic palaeontology

The special morphological terminology used below is based on Turner (1966, pp. 6, 7, figs 2, 6, 7a, b) and Turner (1969, p. N740, fig. E211). To indicate the repositories of specimens studied the following abbreviations are used:

MCZH — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
NHML — Natural History Museum London (formerly British Museum [Natural History]), London.
NHMM — National Museum of Natural History, Geology and Palaeontology Section, Malta.
RGM — National Museum of Natural History, Palaeontology Department, Cainozoic Mollusca (formerly Rijksmuseum van Geologie en Mineralogie), Leiden (The Netherlands).
SMF — Senckenberg Naturhistorisches Museum, Frankfurt-am-Main.
UZM — author's collection (author's original registration numbers are retained) at the University Zoological Museum, Biology Department, Malta.
ZM — author's private collection.

| | |
|---|---|
| Family | Teredinidae Rafinesque, 1815 |
| Subfamily | Kuphinae Tryon, 1862 |
| Genus | *Kuphus* Guettard, 1770 |

*Type species* — *Serpula arenaria* Linné, 1758, by subsequent designation of Gray (1847, p. 188). Linné (1758, p. 787) based this name on *Solen arenarius* of Rumphius (1705, p. 124, pl. 41, fig. d, e) described from Amboina, Moluccas (Indonesia), occurring in mud with gravel.

*Diagnosis* — Non-wood-boring animal with strong muscular collar encircling it just behind the shell valves; intestine passes through the large ventricular bulb of the elongated heart; caecum lacking; very reduced posterior adductor muscle; long separate siphons and solid, non-segmented pallets covered by periostracum which characteristically peels off post mortem. A stout calcite subcylindrical heavy tube bifurcated posteriorly, encloses the elongate animal

| Lithostratigraphy | | | | Chronostratigraphy | | | | |
|---|---|---|---|---|---|---|---|---|
| Formations | Members | Thickness in m | | Series | Stage | | | |
| | | | | | Giannelli & Salvatorini, 1972 | Felix, 1973 | Mazzei, 1986 | Pedley, 1989 |
| Upper Coralline Limestone | Gebel Mbark | 0-165 | | Mioc. | - | - | - | EM |
| | Tal-Pitkal | | | | - | - | - | T |
| | Mtarfa | | | | - | - | - | T |
| | Ghajn Melel | | | | - | - | - | T |
| Greensand | - | 0-15 | | Mioc. | T | - | - | T |
| Clays and Marls Fm. | Upper | 70 | | Mioc. | T | T | T | T |
| | Middle | | | | S | S | S | S |
| | Lower | | | | L | L | L | L |
| Globigerina Limestone | Upper Division | 22-70 | 217 ? | Mioc. | EL | L | A/B | B |
| | Phosphorite Level 2 | 0.1 - 0.5 | | | B | B | A | B |
| | Middle Division | 10 | | | B | A | A | B |
| | Phosphorite Level 1 | 0.2 - 0.6 | | | A | A | A | A |
| | Lower Division | ? | | | A | A | A | A |
| Lower Coralline Limestone | Il-Mara | >140 | | Olig. | - | C | - | C |
| | Xlendi | | | | | | | |
| | Attard | | | | | | | |
| | Maghlaq | | | | | | | |

Fig. 2. The exposed Cainozoic sequence of the Maltese Islands. Formations after Murray (1890), members after Pedley (1989), A - Aquitanian; B - Burdigalian; Ch - Chattian; EL - Early Langhian; L - Langhian; S - Serravallian; T - Tortonian; EM - Early Messinian.

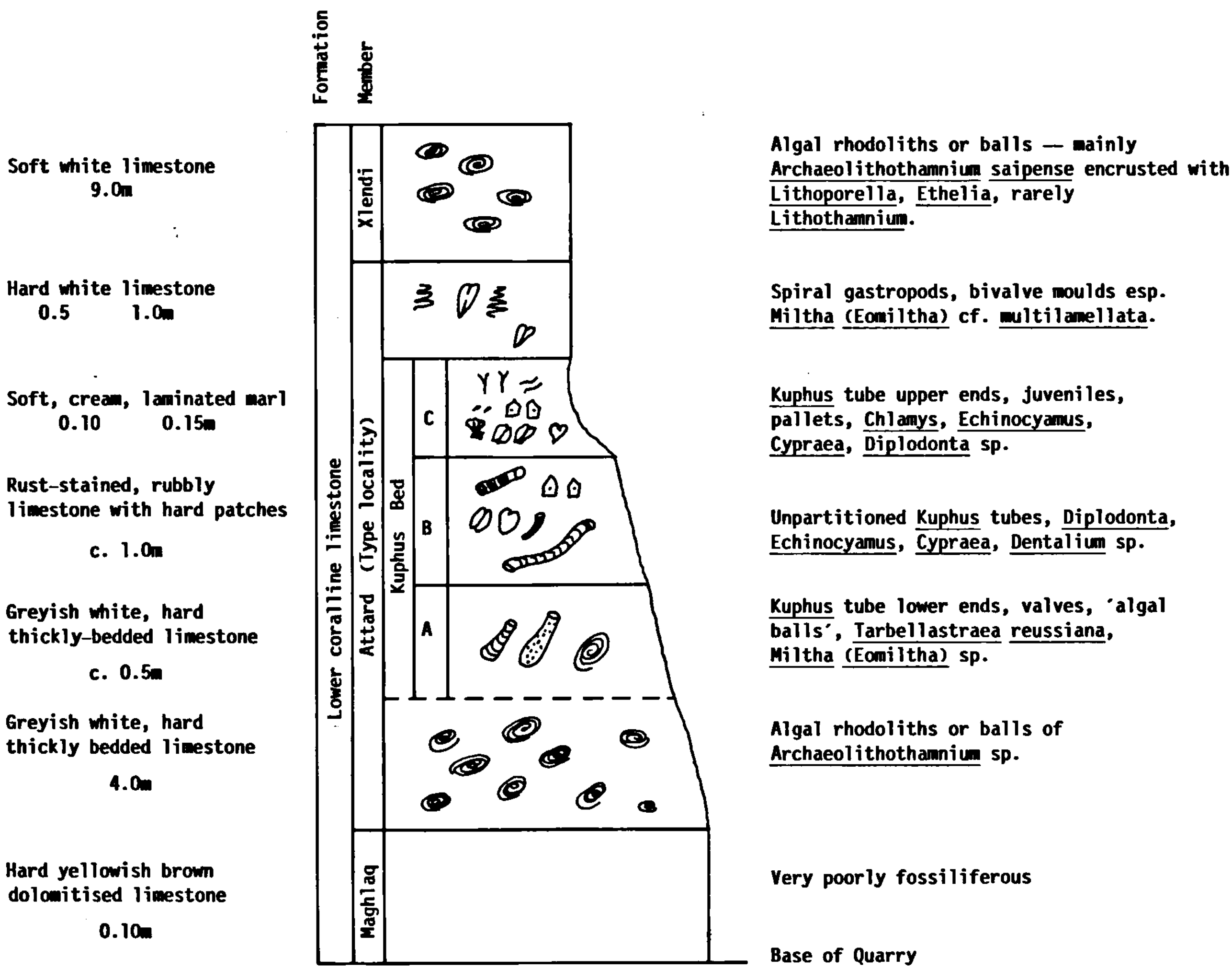



Fig. 3. Schematic lithostratigraphy and faunal content of the Lower Coralline Limestone Formation as exposed at the Wied Incita quarry (Attard, Malta) (not to scale).

and is attached to it solely by the muscles of the pallets and of the siphons.

*Habitat* — Recent *Kuphus* live in mangrove areas of the Indo-Pacific where they occur in burrows in mud or sand with gravel. They are not known to bore into wood. They feed by extending long separate siphons above the bottom and filter feed from the water (Turner, 1966, 1969). The Indo-Pacific affinity of Maltese Cainozoic *Kuphus* and some other local Oligo-Miocene fossils was first described by Zammit Maempel (1979), but if the 'canaliti geniculati vel plus minus reflexi' referred to in Bettz's unpublished manuscript (1794, p. 19) are *Kuphus* tubes, then such affinity was noted by this member of the Order of St. John of Jerusalem almost two centuries earlier (Zammit Maempel, 1982).

*Nomenclature* — *Kuphus* was first figured by Rumphius (1705, p. 124, pl. 41, figs d, e), who illustrated a shelly tube from Amboina, Moluccas (Indonesia) and called it *Solen arenarius* or 'sandpyp'. Seba (1758, p. 182, pl. 94) figured the *Kuphus* animal and called it 'Tuyaux intestines'. Linné (1758, p. 787, paragraph 699) — perhaps considering *Kuphus* to be a serpulid — referred to the animal as *Serpula arenaria*, a name which he subsequently (1767, p. 1266) changed to *Serpula polythalamia*. In 1770, Guettard introduced the genus *Kuphus* for the worm-like mollusc *Solen arenarius* of Rumphius and *Kuphus polythalamia* became the entrenched name for the living species. However, according to ICZN rules, the 1758 name is valid despite Linné's own correction in 1767. Hence, the animal should be referred to as *Kuphus arenarius* (Linné, 1758).

**Kuphus melitensis** sp. nov.
Pl. 1, Pl. 2, Figs 1-10, 12, Pl. 3, Figs 5-15; text-figs 4, 5

1655 petrified serpents of Malta — Worm, p. 90.
?1794 canaliti geniculati vel plus minus reflexi — Bettz, p. 19.
?1805 sea tubes — de Boisgelin, p. 138.
1852 cylindrical tubes — Spratt, p. 8.
1866 large species of *Teredo* — Jones, pp. 152, 153.
1870 large species of *Teredo* — Adams, pp. 266 [footnote 19], 271.
1916 *Magilus grandis* Oppenheim, p. 107.
1973 vertical borings ..... with walls showing rings and pustules on their side — Felix, p. 19.
1977 *Kuphus* — Zammit Maempel, p. 22, pl. 15.
1979 *Kuphus*, *Kuphus* n. sp. — Zammit Maempel, pp. 4, 7, pl. 2, figs 4, 10.
1980 *Kuphus* cf. *polythalamia* — Bosence *et al.*, p. 36.
1982 *Kuphus* — Geys & Beeusaert, pp. 44, 45, fig. 9.
1989 *Kuphus*, sigarri, swaba, terha, dudu — Zammit Maempel, pp. 4, 7, 11, pl. 2, figs 4, 10.
1990 *Kuphus* — Pedley *et al.*, p. 15, fig. 5a.

*Type* — Holotype is a tube fragment with disarticulated valves preserved as moulds at the open end (Pl. 3, Fig. 12); University Zoological Museum, Biology Department, Malta, registration number UZM/K. 206 (leg./coll. G. Zammit Maempel).
Paratypes:
— NHML, no. 40006 (leg./coll. G. Zammit Maempel ZM/K. 106).
— NHMM/Z.M. Collection (leg./coll. G. Zammit Maempel), Wied Incita (Attard, Malta), L.C.L. quarries: K.11, K.20, K.27, K.42, K.47, K.52, K.96, K.200, K.202, K.227, K.229-338.
— RGM (leg./coll. G. Zammit Maempel, Wied Incita (Attard, Malta): RGM 393 030-393 048 (*ex* K.5, K.69, K.89, K.203, K.306-318, K.321, K.325).
— UZM (leg./coll. G. Zammit Maempel), Wied Incita (Attard, Malta): K.1, K.10, K.13, K.14, K.23, K.24, K.30, K.39, K.48, K.53, K.60, K.67, K.101, K.109, K.112, K.204, K.210, K.213, K.215, K.221, K.225, K.302, K.319-326, K.328.
— ZM (author's private collection): K.6, K.22, K.28, K.37, K.51, K.54, K.57, K.72, K.201, K.207, K.213, K.339-350 and numerous other specimens.

*Derivation of name* — After Malta.
*Stratum typicum* — *Kuphus* Beds, Attard Member (Lower Coralline Limestone Formation), Late Oligocene (Chattian).
*Locus typicus* — Wied Incita (Attard, Malta), grid reference 495714.
*Diagnosis* — In comparison to *Kuphus arenarius* the tube is less acute, thicker, more prominently and more regularly annulated. The valves are much smaller, more quadrangular, much thicker and with more prominent and evenly distributed ridges or ribs that occasionally occur in bunches. The pallets are much more delicate, with stalk straighter, flatter and preserved without an awn, and with a proximal cylindrical rod (handle) proportionately larger than that of *K. arenarius*, forming one third to one fourth length of the pallet.
*Description* — The tubes gently taper posteriorly (upwards), are thick walled and thinly laminated (Pl. 1, Fig. 3), calcitic, often tortuous, slightly shiny, greyish-green, smooth surfaced with external annulations (growth rings) (Pl. 1, Fig. 5), with a dull whitish-yellow, smooth internal surface. Structures on and within the tube record information on its environment and past history. Adjoining shells and pebbles leave their imprint on the tube's exterior (Pl. 1, Figs 2, 4; see also Savazzi, 1983, p. 297, fig. 11e). The tube comprises six principal regions (Fig. 4):

— the anterior (lower) end, usually open, but occasionally with hemispherical closure (Pl. 1, Fig. 7);

— the main undivided tube tapering posteriorly (upwards) (Pl. 1, Figs 1, 2, 4, 5, 7; Pl. 2, Figs 3, 12; Pl. 3, Fig. 7). There may be one conical internal closure (Pl. 2, Fig. 7), and several external swellings of tube wall (Pl. 1, Fig. 6; Pl. 2, Fig. 7). Externally, the main undivided tube commonly bears impressions of formerly adjacent gastropods, bivalves and pebbles (Pl. 1, Figs 2, 4) and organic calcareous encrustations around its lower (anterior) region (Pl. 1, Fig. 7; Pl. 2, Fig. 12). During growth, there was often resorption of earlier deposits of the tube;

— the internally longitudinally divided tube (siphonal end) without evidence at surface proximally (Pl. 2, Figs 3, 8-10). Separating the main undivided tube from the distal divided siphonal end is a diaphragm with two adjacent, subequal, subcircular/ovoid openings;

— the externally divided but attached tubes more distally (Pl. 2, Figs 1, 2);

— the region of external bifurcation (Pl. 2, Figs 1, 2). Extruded siphons leave the tube through a resorption area;

— the posterior end of the tube with two distinctly separate siphonal tubes (Pl. 2, Figs 1, 2), their exterior covered with irregular, protruding lamellae (Pl. 2, Figs 1, 3); the exhalent tube is usually smaller than the inhalent one; both may be irregular in

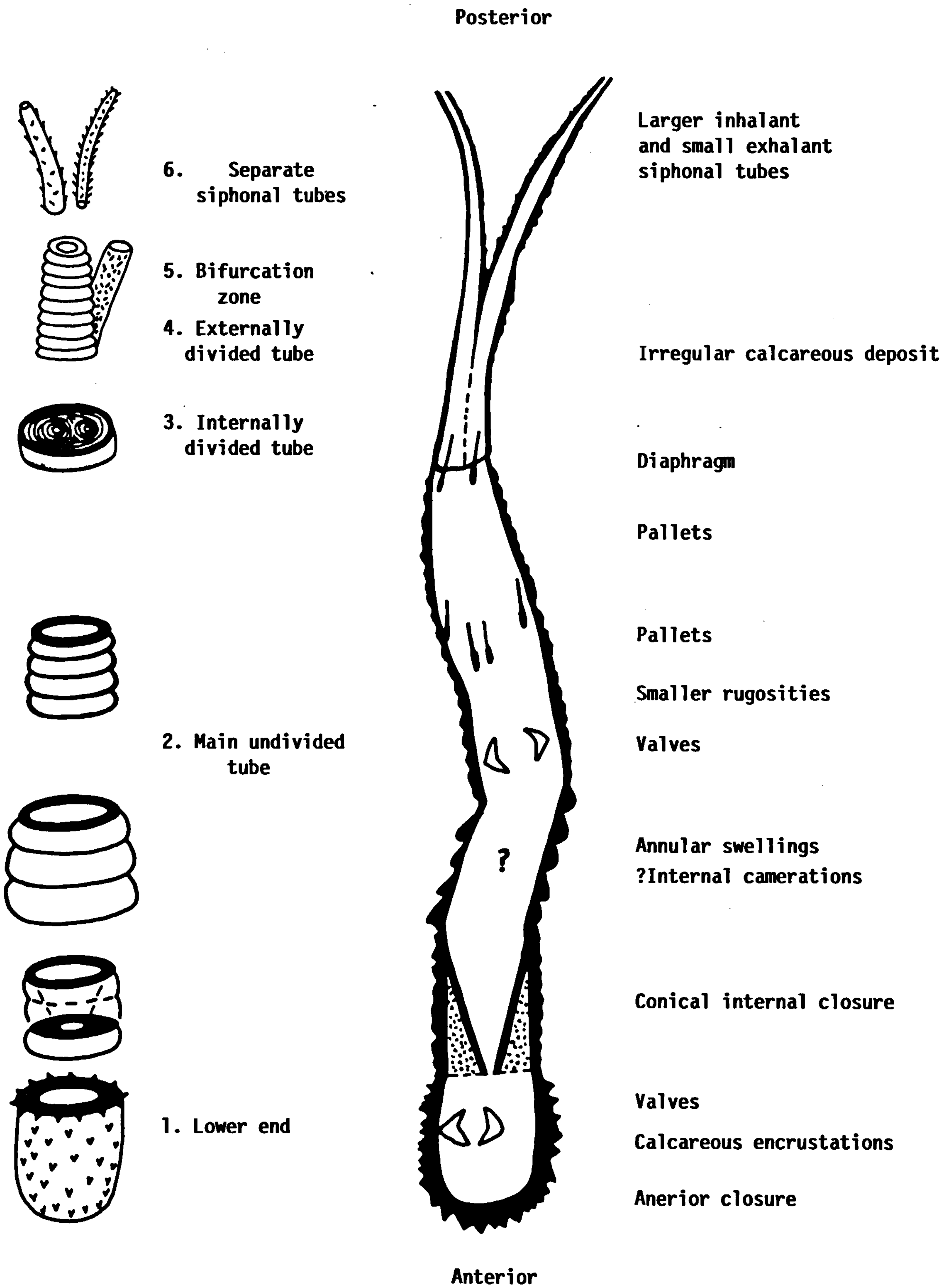



Fig. 4. Schematic reconstruction of *Kuphus melitensis* sp. nov. tube, with indication of levels where pellets and valves have been located in different tubes (not to scale).

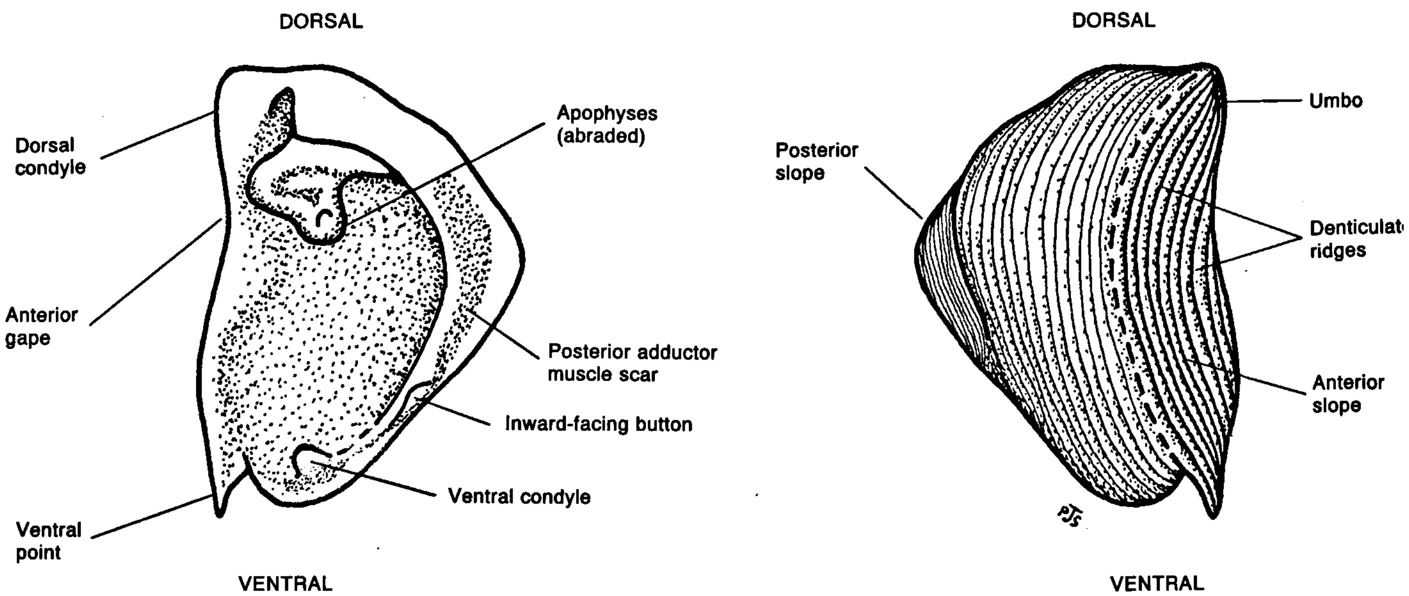



Fig. 5. Reconstruction of the right valve of *Kuphus melitensis* sp. nov. (external and internal views) based on artificial casts.

direction; the lumen in each tube may be as small as 1 mm (Pl. 2, Fig. 4).

The valves of *Kuphus melitensis* are much reduced (Fig. 5), subquadrangular in lateral view and strongly convex; the anterior slope tapering to a point ventrally and maximum width lying at mid point, being always greater than maximum [dorso-ventral] height. The umbones are prosogyrate. The external surface has a sculpture of ventral ribs curving from umbo to ventral point, the ridges are unequal and occasionally bunched forming distinct steps on the shell surface. The inner surface bears a thick arch on its upper edge, which terminates dorsally in a lantern-like apophysis whose surface is abraded in all available specimens. The inner surface of the ventral part of the shell bears a ventral condyle, an inward-projecting boss which lies on the median line; the remaining inner shell surface is smooth, no muscle scars could be identified.
*Measurements* — Height, diameter of valves in apposition and diameter of tube at level of lodgement of valves, all in millimetres [and in that order] gave the following values: 11.0, 12.5, 17.5 [UZM/K.203]; 12.5, 16.0, 21.0 [UZM/K.48]; 13.0, 20.0, 40.0 [UZM/K.204]; 14.0, 10.0, 40.0 [UZM/K.89].

Pallets of *K. melitensis* (Pl. 3, Figs 5-11) consist of a proximal solid cylindrical rod (handle) and a flattened, lamellated, distal portion (stalk). The straight stalk is about three times the size of the handle and lacks the terminal, flattened, lateral protuberance (awn) present in other (Recent) Teredinidae (Fig. 6).
*Discussion* — The following discussion is largely restricted to a comparison of *K. melitensis* with Recent material of *K. arenarius* from the Indian and Pacific Oceans. Comparative hard parts morphology is outlined in Table 1 with the following additional information:

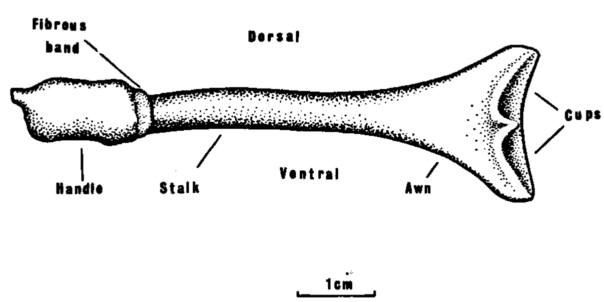



Fig. 6. Terminology of right pallet of *Kuphus arenarius* (Linné, 1758) based on specimen NHML, no. 1933.7.14.1. This pallet lacks the gentle ventral and medial curve of the stalk noted in other Recent specimens.

Tube — A Recent tortuous *K. arenarius* tube in the author's collection at the Zoological Museum (Biology Department, University of Malta, UZM/KK.1) has a vertical height [length] of 675 mm. The circumference and external diameter of its uppermost [posterior] end are 62 and 18 mm, respectively. The

| | *Kuphus arenarius* | *Kuphus melitensis* |
|---|---|---|
| Pallets | | |
| Size | bulkier | more delicate |
| Composition | aragonitic | originally aragonitic, now calcitic |
| Maximal length | 80 mm | 51 mm |
| Awn | present | absent |
| Handle/pallet-ratio | 1 : 3-4 | 1 : 2.5-5 |
| Stalk course | lateral and dorsal convexity | straight |
| Stalk structure | laminated round and eccentric solid rod | laminated round and eccentric solid rod |
| Stalk cross-section | subcircular | subtriangular |
| Maximal diameter of stalk | 4.5 mm | 2.8 mm |
| Tube | | |
| Shape | more acute | less acute |
| Surface | rough, lustreless | smooth, shiny |
| Organic encrustations | absent | present in lower region |
| Annulations | weak | prominent |
| Ridges | wide, irregular | narrow, more regular |
| Inside surface | smooth, with external ridges sometimes reflected | smooth |
| Maximal diameter | 41 mm | 34 mm (49-53 mm if encrusted) |
| Wall thickness | max. 2 mm (locally 4-7 mm) | max. 4 mm (more with encrustations) |
| External anterior closure | hemispherical | hemispherical,'drumstick'-like flattened convexity |
| Valves | | |
| Size | max. 20 mm | max. 14 mm |
| Thickness | max. 1.0 mm | max. 2.1 mm |
| Shape | subtriangular | subquadrangular |
| Ribs | close together, not prominent, regular distribution | widely spaced, prominent, bunched in areas |
| Denticulations | variable | not apparent on peels |

Table 1. Comparison of hard part morphology of *Kuphus arenarius* (Linné, 1758) and *K. melitensis* sp. nov. Data based on several Recent specimens from the Solomon Islands, Philippines, Sumatra, Andaman Islands, and Indian Ocean, and on fossil material collected by the author from the type locality of the latter species.

corresponding measurements at its open lower [anterior] end are 145 mm and 33-41 mm (internal diameter 31-36 mm). The thickness of tube wall at its open lower end is 2-5 mm and is 3.9 mm at 40 mm above the edge. No specimens of *K. melitensis* preserving the bifurcated posterior (upper) end and closed anterior (lower) end have been recovered from the *Kuphus* Beds at Wied Incita.

In *Kuphus arenarius*, the closed anterior end of the tube is invariably associated with an adjoining 1-2 cm wide ring of irregularly scattered sieve-like perforations of the tube. These are analogous to those observed on the lower end [anterior part] of members of the Clavagellacea (genera *Clavagella* Lamarck, 1818 and *Penicillus* Bruguière, 1789) and, presumably, enable the lower end of the sealed-up animal to keep in direct contact with its environment (see also Pojeta & Sohl, 1987, pp. 2, 4). In a Recent tube of *K. arenarius* tube (NHML, no. 1857.11.30.12) these perforations extend also over the two convex calcareous sheets formed by secretion from the two opposite sides of the tube to seal the lower end. When growth of the tube is resumed, the perforations are turned into pits which may remain markedly evident (specimen NHML, no. 66.5.3.I). In some Recent specimens, *e.g.* a tube from Ngela Islands, Solomons (UZM/KK.1) and one from Java in the Wilkinson Collection (NHML, no. 1968.396/2), such pits are scattered over other regions besides areas adjacent to the site of external closure (past or present) (Pl. 2, Fig. 12). Clustered pits detected on the calcareous encrustation enveloping the closed lower [anterior] end of a *K. melitensis* tube (UZM/K.303) seem to be features of the sponge-like surface of the organic overgrowth and not related to the underlying tube surface.

Tube closure — Authors such as Griffiths (1806), Gray (1858), Douglas (1927), Cox (1927) and Tavani (1948) referred to the lower (anterior) end of *Kuphus* tubes as being 'closed'. Investigations have revealed, however, that Recent *Kuphus* tubes are actually open, becoming sealed up only periodically. The first closure seems to take place when the tube is about 50 mm long (observed range: 30-63 mm). All adult *K. arenarius* tubes examined showed evidence of having had 5-6 irregularly spaced closures which probably represent periodical 'growth halts' or periods of rest with added protection to the animal. Possibly, only adults reaching maturity and maximum development have their lower end permanently sealed by what Douglas (1927, p. 3) called 'two arched laminae'. These are very clearly evident in the *Kuphus arenarius* tube NHML, no. 1857.11.10.30.12. Possibly, with age, the animal loses its power of resorbing the thin calcareous seal or else may be in need of extra protection provided by the closed lower end or, perhaps, there is no need for further burrowing into the sediment.

In addition to the 'external' (anterior-end) closure just mentioned, Recent *Kuphus* sometimes develops a series of somewhat similar, but internal, diaphragms forming 'camerations'. In view of the infrequent occurrence of these structures, such closures probably represent abnormal growth halts, *i.e.* periods of great stress or times of severe hostile environmental conditions either above or below the sediment/water interface. The phenomenon of cameration was first noticed by Home (1806) on the Sumatran 'giant wormshell' brought back by Griffiths (1806; see also Queckett, 1860). Junghuhn (1854, pp. 67-70, figs 1-9) noted a similar phenomenon inside a fragment of a Recent tube from Java, ascribed by him to a new species of mollusc, called 'Kurang surumbang'. In spite of his enigmatic description of the tube being 'habitus ceratatoides sed sipho nullius', the tube is still considered to be that of *Kuphus arenarius*, for his 'sipho nullius' probably refers to the specimen available rather than to the species.

A series of posteriorly (upwardly) receding camerations was observed in two comparable fossil tubes (NHML, no. L.25131, post-Pliocene, Gulf of Suez, and NHML, no. L.70352, Pleistocene, Tanzania) in which cameration is associated with localised external tube thickening, massive invasion by encrusting organisms and with pronounced annular constrictions in between. X-radiography of *Kuphus* tube NHML, no. 25132 has shown the swellings to coincide always with the chambers and the constrictions with the diaphragms (Pl. 2, Figs 13, 14). It is possible that the above-mentioned encrustations could have been the stimulus inducing the animal's upward withdrawal and the consequent formation of the upward-progressing diaphragms. Another possible stimulus could have been the choking effect produced by the sudden and excessive deposition of sediment on the sea floor. To relieve itself of this life-threathening situation, the animal probably extended its already unduly lengthened (progressively tapering) tortuous siphonal tubes, rendering them still less functional but more susceptible to breakage. It is probable that detachment of these fragile parts stimulated the animal to rebuild wider siphonal tubes and possibly also to move upwards in the tube, building a false bottom (diaphragm) beneath it. This might also explain the abundance of narrow-bored siphonal tube fragments (less than 1 mm internal diameter) in the uppermost section ['C' in Fig. 3] of the Attard *Kuphus* Beds (Pl. 1, Fig. 1).

Somewhat analogous, but more pronounced, regular and uniform, encircling swellings and constrictions of the tube occurred in two Maltese Cainozoic specimens (Pl. 1, Fig. 6). Massive infilling of the tubes prevented X-ray investigation. The swellings showed evidence of the usual encrustations (? calcareous algae) associated with lower [anterior] ends. Some other Maltese tubes bear very pronounced, localised, irregular thickenings (maximum thickness 10 mm) due to layers of the organic encrustation (Pl. 2, Fig. 12), noticed also in Red Sea specimens (NHML, no. 25131; Pl. 2, Fig. 13). A completely different (conical) type of internal tube closure which has never been recorded before in Recent or fossil tubes, was discovered in two fragmentary Maltese specimens. None of the tube fragments bears any encrustation but in one the closure is associated with a localised slight swelling of the wall (Pl. 2, Fig. 7). A longitudinal section of this tube shows that the closure is attained by the wedge-like over-development of one of the innermost dark, translucent layers that alternate irregularly with white opaque layers to form the tube wall (Pl. 2, Figs 7-10) and that the localised tube swelling is the result of the additional over-development of the white layers.

Preservation of tubes — As stated, *K. melitensis* tubes complete with bifurcated upper (posterior) end and a closed lower (anterior) end are not known from Maltese Cainozoic deposits. All tubes are fragmented, with parts ranging in size from 40 to 300 mm. Strong vibrations resulting from explosives used in quarrying the limestone often dislodge the tubes from their very hard matrix and increase fragmentation. Tubes that have not been loosened by the explosives cannot be extracted from the indurated matrix of the lowermost division ['A' in Fig. 3] of the *Kuphus* Beds (Pl. 3, Fig. 7).

Calcareous encrustations of tube — A thick calcareous encrustation, having a sponge-like surface texture and forming localised uneven swellings (Pl. 2, Fig. 11), envelops all lower regions (anterior parts) of *K. melitensis* tubes (*e.g.* UZM/K.302 and K. 206). Only very rarely does it extend to a level higher than diaphragm (UZM/K. 213). Protruding perpendicularly from its surface are numerous, irregularly scattered conical tubercles with a height of about 2.5 mm and a maximum base diameter of 1.8 mm (Pl. 1, Fig. 7; Pl. 2, Fig. 11). They resemble stalactitic 'thorns' and like them exhibit a central opening (sometimes two or three) when broken or abraded. The underlying tube wall surface is neither pitted nor in any way affected by the encrusting growth (Pl. 2, Fig. 11), so that their openings cannot be related to the numerous tiny borings observed in the hard infill of the fragmented cylinders (Pl. 3, Fig. 12). The encrustation resembles that by calcareous algae, but its exact nature is still unknown. Calcareous filaments connecting some of the conical structures (Pl. 2, Fig. 11) suggest overgrowth to be of organic origin, possibly encrusting organisms with aragonitic shell that has since disappeared. Such encrustations have not been recorded on Recent *Kuphus* tubes.

Calcium carbonate resorption and deposition — *Kuphus* possesses great powers of resorption and deposition of calcium carbonate. The repair of fractures is preserved (NHML, no. 1968.396/2). The extruded siphons, which leave the main tube through a resorption area, become covered with rough, lustreless calcite (Pl. 2, Fig. 1). Resorption also takes place at strong angulations of the undivided tube or siphonal tubes (*e.g. K. arenarius* NHML, nos 1968.392/2 and 5). 'Growth halts' (interruptions in growth) and subsequent re-activation are also recorded on the tube surface. After a halt, tube regeneration does not proceed from the external edge of the old tube but from its inner surface at a short distance from the edge ('cone-in-cone' type structure). This results in a very slight overhang of the old wall with the production of a characteristic encircling fissure and a localised constriction of the tube surface (Pl. 2, Fig. 12). In addition, the calcareous inner lining deposited on tube wall plugs the ring of sieve-like perforations above the edge of the tube, turning these into mere pits (NHML, no. 1857/11.30.12, *Kuphus arenarius* tube with closed lower end; NHML, no. 66.3.5.1, *K. arenarius* tube with open lower end). As a result of the animal's renewed activity, the convex outwards seal closing the lower end is forcibly shattered (probably with the assistance of partial resorption of the seal) and the fragmented very thin eggshell-like material from the shattered seal is at times found adhering to the outside of the tube wall at this level (*K. arenarius* tube NHML, no. 1910.4.8.1). Also, since penetration of the seal is eccentric, the tube shows a more or less marked angulation just beyond such 'growth halt' with external closure (Pl. 2, Fig. 11).

Abnormality — A partitioned siphonal tube with patent canals (K.72) exhibits sudden dilatation of their tube walls with formation of an internal sacculation - first on one (maximum diameter 10 x 8 mm) and then immediately on the other (maximum diameter 12 x 10 mm). This resulted in partial detachment of the two siphonal tubes with evidence at surface. The abnormality is thought to reflect underlying pathology of the animal's siphons (? localised growth) and would have presumably prevented the animal from extending or withdrawing its siphons.

Valves — Previous authors (*e.g.* Gray, 1858; Calman, 1926) have commented on the absence of shell valves from Recent *Kuphus* tubes. No evidence of such structures was found within the 405 mm long tube with closed lower end (NHML, no. 1857.11.30.12) when this was opened at the time (see note attached to above-mentioned tube). As the possibility of the phenomenon of calcium carbonate resorption in adult *Kuphus* tubes with closed lower end was not then considered, Calman (1926) suggested that the *Kuphus* animal represented a metamorphosed adult form of another teredinid species, such as *Dicyathifer mannii* (Wright, 1866), which in early life bore into wood with the valves, but which on attaining adult form, shed these structures and changed its substrate from wood to mud or sand with gravel. Not all *Kuphus* with closed lower (anterior) end lose their valves, *e.g.* NHML, no. 1857.11.30.12. Another 70 mm long *K. arenarius* with closed lower (anterior) end in the Natuurhistorisch Museum Rotterdam (Kastanjesingel Collection), however, yielded both valves and pallets when opened by Arie Janssen, the curator of Cainozoic Mollusca at the Natural History Museum Leiden (pers. comm., 1971). It is possible that NHML, no. 1857.11.30.12 and the specimen referred to by Calman contained an old animal and that the Rotterdam specimen was merely a young animal with a temporary closure of its lower (anterior) end enjoying the advantages of one of its temporary 'growth halts'. It is not possible to ascertain whether any of the Cainozoic *Kuphus* with closed lower end to tubes did lose their valves, but valves were present in the only fossil tube with evidence of a closed lower end and whose inside could be examined (UZM/K.204). Denticulations on the ribs of the anterior slope of some Recent *Kuphus* valves vary in shape according to their position on the valves. In the dorsal region they are fine triangular projections arising from the external border of the ribs, directed outwards; in the middle region of the valve, they are nodular and swell on either side of the rib, whilst in the ventral region they are flattened, round-edged, blade-like structures arising from the inner side of the rib and directed inwards towards the gape. They probably serve as graters, beaters and scrapers/scoopers of mud, respectively. It was not possible to identify any such structures on the rubber peels of the Maltese *Kuphus* valves.

Preservation of valves — *Kuphus melitensis* valves are all preserved as moulds, indicating that the composition was probably aragonitic. Cavities left by the aragonitic valves provide a weak area in the otherwise solidly infilled tubes which tend to break at this level to expose the internal/external moulds of the valves. Most valves are in apposition (UZM/K.48, 89, 200-204), located either high up in the tube almost blocking its internal diameter (Pl. 3, Figs 13-15) or lower down occupying half its width (Pl. 3, Fig. 12). The position of the fossil valves undoubtedly depends on the position and level of the animal, as well as on the inclination of the tube at the time of the animal's death. Post-mortem shrinkage of the animal may also be responsible for the high position of some of the fossil valves inside the tube (Pl. 3, Figs 13-15). In life, however, the valves are normally close to the lower (anterior) end, and were found to be still occupying this position in specimen UZM/K.204, with closed anterior (lower) end.

The eight Recent *Kuphus arenarius* animals (from Solomon Islands) examined by the author have valves that are much larger than those of any of the *Kuphus melitensis* (ZM/K.34, ZM/K.48, ZM/K.106 (= NHML, no. 40006), ZM/K.200, ZM/K.201, ZM/K.202, ZM/K.203, ZM/K.206 (holotype = UZM/K.206), and ZM/K.213).

Pallets — The pallets of *Kuphus arenarius* are internal structures attached to the rest of the animal by the sleeve muscles and to the tube by their retractor muscles. Presumably, when danger threatens, first the siphons and subsequently the pallets, are withdrawn. The distal ends of the two awns are placed in contact with each other forming a protective canopy over the animal at a level just beneath the diaphragm. The lateral convexity of the Recent *Kuphus* stalk helps facilitate such an apposition and accommodate the animal in protecting itself against external threats. Each pallet of *K. arenarius* consists of a short, wide, proximal cylindrical rod (handle) and a narrower cylindrical extension (stalk) separated from each other by an obliquely placed encircling fibrous band. At the distal end of the stalk is a triangular flattened development (awn) that generally encloses at its distal end (base of triangle) one or more cavities (cups, pockets) (Fig. 6). The stalk passes into the awn without discontinuity (see also Moll, 1952, p. 81), gently curving ventrally and medially along its course (NHML, no. 1857.11.30.12; Pl. 3, Fig. 1). The distal cavity or cup within the awn is thereby divided completely (NHML, no. 1933.7.14.1) or partially (NHML, no. 1857.11.30.12) into a larger dorsal and a smaller ventral pocket. The course of the stalk within the awn can usually be followed as a marked protuberance running along its flat inner (medial) wall (NHML, no. 57.11.30.12; Pl. 3, Fig. 1), often terminating as a distinct knob at its distal edge (NHML, no. 1933.14.7.IV). The lateral wall of the awn is shorter and more inflated than the medial one, giving rise to the 'cup' (Pl. 3, Fig. 1; text-fig. 6). In some specimens (NHML, no. 1933.7.14.I), the lateral wall bears a median cleft or indentation at its distal margin. In some specimens, this is accompanied by lateral developments within the cup, somewhat suggestive of the two tube-like structures developed by some species of the genus *Teredo* Linné, 1758. The absence of an awn from all fossil stalks recovered and the presence of fossil pallets jamming the narrow-bore siphonal canals of UZM/K.213, 215, 219 and 221 (see Pl. 3, Figs 5, 6, 11) suggest that pallets of *K. melitensis* never had an awn. They could consequently have had quite a different function to perform, an opinion supported also by the absence of the characteristic lateral and dorso-ventral curvatures noticed in Recent pallet stalks. Sectioning of the pallet stalk of a Recent *K. arenarius* (NHML, no. 1933.7.14.IV) and radiography of the pallet awn of another such specimen (NHML, no. 1933.7.14.I) have revealed that the stalk increases in diameter by the addition of successive laminations along its external side (Pl. 3, Fig. 2), and thus indicates that the pallets are covered, during life, by tissue comparable with mantle tissue, capable of carbonate excretion, whilst the awn does so by the addition of successive laminations along its distal border (Pl. 3, Fig. 3). An accidental fracture of a fossil pallet stalk (UZM/K.126; Pl. 3, Fig. 10) revealed its structure to be identical to that of the Recent *Kuphus* (NHML, no. 1933.7.14.IV; Pl. 3, Fig. 2), both being formed by the accretion of laminations (thick at centre, tapering off laterally) around an eccentric (medial) solid core. A calcareous laminated deposit encircles a fossil pallet UZM/K.126 (Pl. 3, Fig. 9) obliquely, forming a projecting hood-like structure on one of its sides at the junction of stalk/handle. It seems to be analogous to the similarly situated and similarly angulated, tough, fibrous band present in *Kuphus arenarius* pallets (NHML, no. 1933.7.14.1; see also Fig. 6). A number of grooves radiating outwards and upwards from the convex base of the handle provided better attachment for the sleeve muscles of the *K. melitensis* pallet. In Recent *Kuphus*, better attachment of the sleeve muscles is procured by a more rugged handle and by one or more anteriorly-directed projections of the edge of the handle (Fig. 6). It was also observed that brackish water *Kuphus arenarius* tend to have much thicker and larger pallets than specimens from marine environments and that the pallets of marine *K. melitensis* differ markedly in size and shape from the homologous but bulkier structures possessed by its modern congener (Pl. 3, Figs 1, 5-11; text-fig. 6) from brackish waters.

Preservation of pallets — Pallets are invariably preserved as calcite stalks with handle; most rest on the lithified infill of the unpartitioned tube (Pl. 3, Fig. 7); in one case, a set of pallets was found adhering to the inside of the uppermost region of an empty tube cemented in position by minute sparry crystals of calcite; other sets jam the siphonal canals of tube fragments UZM/K.213 (Pl. 3, Fig. 5), UZM/K.215 (Pl. 3, Fig. 11), UZM/K.219 and UZM/K.221 (Pl. 3, Fig. 6), whilst a few others were found free-lying. The handles of pallets UZM/K.213 and 221 project anteriorly about 1 cm beyond the diaphragm into the empty unpartitioned tube, being held in position by minute crystals of calcite. Some free-lying pallets (UZM/K.214, *Kuphus* Bed, Middle Division = 'B' in Fig. 3) have their handle encrusted with calcite crystals and their stalk free of any such encrustation, thus indicating that they too once occupied a position in the siphonal canals similar to that of UZM/K.213 and 221, but became liberated from their tube.

## Palaeoecology

Three entire *Kuphus* animals collected for the author by J. Pepys-Cockerell from Ngela Island (British Solomon Islands Protectorate), where the animal is eaten and called 'lombio', were found at the entrance to a small brackish water stream running through mangrove swamps. The animals were collected at approximately 2000 metres from Biota on the northern entrance to the Boli passage in the Ngela group of islands. They were living in mud containing gravel and small pebbles (1 cm diameter) in a water depth of 30-60 cm with the tip of their shell and their soft tissue siphons projecting about 5 cm above the sediment surface. Although the animal's body is of a gun-metal colour, the projecting siphons are bright orange-brown, much resembling the roots of decayed trees and therefore well camouflaged (J. Pepys-Cockerell, pers. comm. 12.3.1973). A 370 mm long unbroken *Kuphus* tube from Java (NHML, no. 1968.386/1) has epibionts attached to its upper [posterior] and middle third. These include post-mortem attachment of the bryozoan *Membranipora* sp. and non-porous barnacles that need fully marine conditions for survival. This shows that *Kuphus* tubes (even of considerable length) may become partly exhumed or completely dislodged intact from their substrate. Fragmented tubes may be buried 'a few feet down', for a note by Bertram B. Osmaston of the Imperial Forest Service, the collector and donor of the large end of *Kuphus arenarius* tube NHML, no. 1910.8.4.1, records that it was 'dug up a few feet below the surface, on the beach in estuarian mud, at Hope Town, Post Blair, Andaman Is., Indian Islands'.

Old records quote *K. arenarius* inhabiting 'mangrove swamps' (von Martens, 1883, p. 218; Oppenheim, 1916, p. 108, footnote 14), 'mud with gravel' (Rumphius, 1705, p. 124, SE Ceram), 'sand with gravel' (Dillwyn, 1817, pp. 1087, 1088; Fischer, 1887, pp. 1158, 1159; Oostingh, 1925, p. 319, Malay Archipelago), 'hard sand' (Sivickis, 1928, pp. 293, 294, pl. 3, fig. 14, Mindaro) and 'coral reefs' (Junghuhn, 1854, pp. 64-70, Java, possibly transported; Hedley, 1895, pp. 464-466; 1898, p. 96). As insufficient ecological information is given in these old records of *Kuphus* finds and as they ignore completely the presence or absence of epibionts, it is not known if these were living at the time of exhumation or whether they were living on dead or live tubes.

Epibionts invaded also a number of fragmented tubes of *K. melitensis* in the upper division of the *Kuphus* Beds at Wied Incita. This unit represents an extensive elongation of an algal-rich calcareous sediment laid down under normal marine conditions. The tubes were subvertical and mostly buried in the sediment with their upper parts exposed. It is not clear whether colonisation by epibionts took place *in situ* while *Kuphus* was living or shortly after death or after the tops had been broken off and reworked into the overlying sediment. In the last case, the broken tops could have been exposed on the sea floor for a considerable period before being buried.

In none of the Maltese *Kuphus* Beds was any wood or wood-like material found associated with *Kuphus* tubes. Unlike other Teredinidae, Recent and fossil *Kuphus* is not known to (have) bore(d) in wood. The fossils associated with Maltese Cainozoic *Kuphus* (echinoid *Echinocyamus*, bivalve *Chlamys*, gastropod *Cypraea* and scaphopod *Dentalium* at Wied Incita, and *Echinocyamus* and a coral reef at San Pawl tat-Targa) are indicative of a shallow, warm, fully marine environment. Associated fossils of other Cainozoic occurrences also suggest a normal salinity marine environment (Cottreau, 1912; Cottreau & Collignon, 1924; Rutsch, 1942; Jung, 1971).

## PALAEOGEOGRAPHY

Geographical and ecological conditions for the genus *Kuphus* have altered considerably since early and middle Cainozoic times. From an almost world-wide distribution in tropical and subtropical shallow seas (Fig. 7), the genus is now restricted chiefly to the brackish waters and mangrove swamps of the Indo-Pacific region (Zammit Maempel, 1979, fig. 7). Tavani (1948, p. 9) stressed the effect climatic changes had in shifting the distribution of *Kuphus* south of the equatorial line. Recent *Kuphus* is most abundant around the Solomon Islands and the East Indies, but it does not figure in the faunal list of the mangrove swamp forests of the Indo-West-Pacific region compiled by Macnae (1968). *Kuphus* has disappeared from the Mediterranean and the Caribbean since the middle Cainozoic. As in those times, modern *Kuphus* still inhabits shallow warm sea waters, but it has now moved south of the equatorial line and has adapted itself, almost exclusively, to brackish water conditions and mangrove swamps.

## ACKNOWLEDGEMENTS

Deep gratitude is expressed to Drs S.R.A. Kelly (Cambridge), P.S. Crowther (Bristol), R.P.S. Jefferies, N. Morris, and C.P. Nuttall (all Natural History Museum, London), R.D. Turner (Harvard), T.J. Palmer (Aberystwyth) and A.W. Janssen (Leiden) for help and advice; Drs R.D. Turner (Cambridge, Massachusetts), N. Tebble (then London), A. Zilch (Frankfurt) and P. Jung (Basel) for allowing access to collections in their care; the late

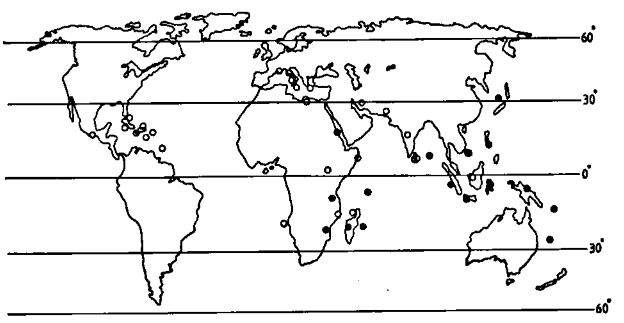



Fig. 7. Geographical distribution of Recent (black dots) and fossil (open dots) *Kuphus*.

J.P. Pepys-Cockerell for setting up two expeditions (1972-73) to locate *Kuphus* colonies and collect specimens for the author; Dr H.E. Coomans (Amsterdam), Dr E. Gittenberger (Leiden), A.W. Janssen (Leiden), A. Capart (Brussels), R. Kelias (Berlin), C.E. Palmer (Glasgow), J. Knudsen (Copenhagen), Miss Dobson (London), R.M.C. Eagar (Manchester), J.V. Harrison (Oxford), A. Radwanski (Warsaw), T. Harrison (Kuching, Malaysia), Rev. P.L. Seitz (Kontum), Nguyan Van Xuan (NhaTrang) and Fr. Truong (Dalat) for data on museum material; Prof. J.A. Douglas, R.L. Merklin, L.A. Korobkov and G. Tavani for field data from Iran, Russia, Cyrenaica and Somalia; Dr F.E. Eames (Middlesex) and Dr P.E.P. Deraniyagala (Sri Lanka) for information about fossil material recovered by them from Iraq and Sri Lanka, respectively; Drs L. Giannelli and G. Salvatorini (Pisa) for reporting on the micropalaeontology of the *Kuphus* Beds sediment, Dr R.J. Davis (London) on the mineralogy of Maltese *Kuphus* tubes and Mr C.P. Palmer (London) on the associated scaphopods; Prof. Dr C.-D. Reuther (Berlin) for helpful discussions on the tectonics affecting *Kuphus* Beds at Wied Incita, Prof. J.P. Schembri, Miss M. Dimech and Miss Brown for help in one of the drawings; Marquis J.P. Testraferrata Bonici for the photography and my sons Ivan, Mark and Joe and daughter Anna for their assistance in the collection of specimens (1964-79). Their help is gratefully acknowledged.

## References

Adams, A.L., 1870. Notes of a naturalist in the Nile Valley and Malta. Edinburgh (Edmonston & Douglas), 295 pp.

Bettz, A., 1794. Discorso accademico delle petrificazioni di Malta del Sig. Abbate Bettz, Gerosolimitano Bavaro, letto dal medesimo nell'Accademia Letteraria di Malta il di' 6 Ottobre 1794. Valletta (National Library), Malta, manuscript no. 349, 34 pp. (unpublished).

Boisgelin, L. de, 1805. Ancient and Modern Malta. London (Richard Philips), 1: lviii + 326 pp., map, 14 pls; 2: vi + xxxi + 258 pp.

Bosence, D.W.J., H.M. Pedley & E.P.F. Rose, 1980. Field Guide to the Mid-Tertiary carbonate facies of Malta. London (Palaeontological Association), 88 pp.

Calman, W.T., 1926. Exhibition of a specimen of the giant Teredo. — Proc. linn. Soc. London, 467: 5.

Cossmann, M., 1921. Synopsis illustré des mollusques de l'Éocène et de l'Oligocène en Aquitaine. — Mém. Soc. géol. Fr., Paléont., 55: 23-116, pls 11-18.

Cottreau, J., 1912. Observation sur les terrains tertiaires de la Côte entre Sousset et l'Anse du Grand Vellat (Bouches du Rhône). — Bull. Soc. géol. Fr., (4)12(5-6): 331-342.

Cottreau, J., & N. Collignon, 1924. Les couches dites à 'Magilus grandis' de l'île de Mokamby, province de Majunga - leur âge, leur extension sur la Côte Ouest et à l'extrème Sud de Madagascar. — Bull. Soc. géol. Fr., (4)24: 278-280, pl. 24.

Cox, L.R., 1927. Neogene and Quaternary Mollusca from Zanzibar Protectorate. *In*: Report on palaeontology of the Zanzibar Protectorate based mainly on the collection made by G.M. Stockley A.R.C.S., D.I.C., F.G.S., Government Geologist, 1925-26, Zanzibar. Zanzibar (Government of Zanzibar), pp. 13-102, pls 3-19.

Deraniyagala, P.E.P., 1969. The fossil giant Teredo of Ceylon: new subspecies. — J. r. Asiat. Soc. (Ceylon Branch), n.s., 13: 39-41, 1 fig., 1 pl.

Dillwyn, L.W., 1817. A descriptive catalogue of Recent shells arranged according to the Linnean method, 1-2. London, pp. 1-580 (1), 581-1092 + 29 pp. (2).

Douglas, J.A., 1927. Contribution to Persian palaeontology: Kuphus arenarius from the Miocene of Persia. London/ Oxford (Anglo-Iranian Oil Company Ltd.), 5 pp.

Felix, R., 1973. Oligo-Miocene stratigraphy of Malta and Gozo. Wageningen (Veeman), 104 pp., 8 figs, 7 pls.

Fischer, P., 1880-87. Manuel du conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivents et fossiles. Suivi d'un appendice sur les brachiopods par D.P. Oehlert, avec 23 planches contenant 600 figures desinnées par S.P. Woodward. Paris (F. Savy), xxv + 1369 pp., 1188 figs, map, 24 pls.

Gabb, W.N., 1873. On the topography and geology of Santo Domingo. — Trans. Am. phil. Soc. Phil., n.s., 15: 49-259, 2 maps.

Gabb, W.N., 1881. Descriptions of Caribbean Miocene fossils. — J. Acad. nat. Sci. Phil., (2)8: 337-348, pls 44, 45.

Geys, J.F., & J.F. Beeusaert, 1982. Malta en Gozo: Oligoceen en Mioceen op een mediterrane eilandengroep. — Gea, 15(2): 41-49, 18 figs.

Giannelli, L., & G. Salvatorini, 1972. I foraminiferi planctonici dei sedimenti terziari dell' arcipelago maltese, 1. Biostratigrafia del 'Globigerina Limestone'. — Atti Soc. Tosc. Sci. nat., Mem., (A)79: 49-74.

Gray, J.E., 1847. A list of the genera of Recent Mollusca, their synonymy and types. — Proc. zool. Soc. London, 15(178): 129-219.

Gray, J.E., 1858. Observations on the genus Furcella Oken, a conchifer without concha or normal valves, and on the genera Teredo and Chaena. — Proc. zool. Soc. London, 25(342): 243-248, pl. 39.

Griffiths, J., 1806. Description of a rare species of worm shell discovered at an island lying off the north-west coast of the Island of Sumatra in the West Indies. — Phil. Trans. r. Soc. Lond., 96: 269, pl. 10, figs 1-5; pl. 11.

Guettard, J.E., 1770. Mémoires sur différentes parties des Sciences et des Arts, 3. Paris, pp. 139-143, pl. 69, fig. 8.

Hedley, C., 1895. Conchological notes. — Proc. linn. Soc. NSW, 23(1): 91-96.

Hedley, C., 1898. Further notes on Australasian shipworms. — Proc. linn. Soc. NSW, 23(1): 91-96.

Home, E., 1806. Observations on the shell of the sea worm found off the coast of Sumatra, proving it to belong to a species of Teredo; with an account of the anatomy of Teredo navalis. — Phil. Trans. r. Soc. Lond., 96: 276-292, pl. 12, fig. 4; pl. 13.

Jones, T.R., 1866. Notes on some specimens from Malta. Appendix to: F.W. Hutton. On the physical geology of Malta. — Geol. Mag., 3(22): 151, 152.

Jung, P., 1971. Fossil mollusks from Carriacou, West Indies. — Bulls Am. Paleont., 61(269): 147-262, 2 tabs, 24 pls.

Junghuhn, F., 1854. *In*: L. Arnold (ed.). Java, seine Gestalt, Pflanzendecke und innere Bauart, 3. Leipzig (J.K. Hasskarl), 316 pp., 58 figs.

Linné, C. von, 1758. Systema naturae per regna tria, 1. (10th edition). Holmiae (Laurentii Salvii), iv + 824 pp.

Linné, C. von, 1767. Systema naturae, 1(2) (12th edition). Holmiae: 533-1327.

Macnae, W., 1968. Account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *In*: F.S. Russell & M. Yonge (eds). Advances in marine Biology, 6. London/New York (Academic Press): 73-270, 76 figs, 2 tabs.

Martens, E. von, 1883. Die Weich- und Schaltiere gemainfasslich dargestellt. Leipzig (Fentag)/Prag (Tempsky), iv + 327 pp., 205 figs.

Maury, G.J., 1925. A further contribution to the palaeontology of Trinidad. — Bulls Am. Paleont., 10(42): 96, pl. 18, figs 9, 10.

Mazzei, R., 1986. The Miocene sequence of the Maltese Islands: biostratigraphic and chronostratigraphic references based on nannofossils. — Atti Soc. ital. Sci. nat., Mem., (A)92(1985): 165-197, 3 figs, 1 tab., 3 pls.

Moll, F., 1952. The classification and distribution of the Teredinidae. *In*: Xylophages et pétricoles ouest africain. — Cat. Inst. fr. Afr. noire, 8: 68-123, pls 11, 12.

Murray, J., 1890. The Maltese Islands with special reference to their geological structure. With geological map, two lithographic plates and woodcuts. — Scott. geogr. Mag., 6: 449-488, 6 figs, map.

Oostingh, C.H., 1925. Report on a collection of Recent shells from Obi and Salmahara (Moluccas). — Meded. Landb. Hogeschool Wageningen, 29(1): 382 + 1 pp.

Oppenheim, C.H., 1916. Über die Tertiärbildungen von Deutsch-Ostafrika. — Z. dt. geol. Ges., 68: 103-110.

Pedley, H.M., 1989. Controls on Cenozoic carbonate deposition in the Maltese Islands: review and reinterpretation. — Mem. Soc. geol. It., 38 (1987): 81-94.

Pedley, H.M., D. Bosence, C. Dart & S. Pratt [1990]. Field Guide to the Cenozoic Platform Carbonates of the Maltese Islands. Field Trip Guide, 54 pp., 22 pls. (unpublished handout).

Pojeta, J. Jr., & N.F. Sohl, 1987. Ascaulocardium armatum (Morton 1833), new genus (late Cretaceous): the ultimate variation on the bivalve paradigm. Mem. Paleont. Soc., 24: 77 pp., 42 figs.

Queckett, J., 1860. Catalogue of the contents of the Museum of the Royal College of Surgeons of England, 1. Plants and invertebrate animals in the dried state. London (Taylor and Frances).

Rumphius, G.E., 1705. D'Amboinische Rariteitkamer. Amsterdam, 30 + 340 + 43 pp., 60 pls.

Rutsch, R.F., 1942. Die Mollusken der Springvale Schichten (Obermiocaen) von Trinidad (British West Indies). — Verh. naturf. Ges. Basel, 54: 96-186, 2 figs, pls 3-9.

Savazzi, E., 1983. Adaptations to tube dwelling in Bivalvia. — Lethaia, 15: 275-297, 21 figs.

Seba, A., 1758. Locuplatissimi rerum naturalium thesauri, 3. Amsterdam (Jausonio-Waesbergiosa), 212 pp., 116 pls.

Sivickis, P.B., 1928. New Philippine shipworms. — Phil. J. Sci., 37(3): 285-298, 3 pls.

Spratt, T.A.B., 1852. On the Geology of Malta and Gozo. Malta (The Governor = Wm. Reid) Daily Mail Office, 24 pp., maps.

## PLATE 1

*Kuphus melitensis* sp. nov., Lower Coralline Limestone Formation (Late Oligocene, Chattian), Wied Incita quarry, Attard (central Malta).

Fig. 1. Detail of *Kuphus* Beds; tubes penetrating strata subvertically. Scale bar equals 53 mm (= diameter of white ring on lens-cover).

Fig. 2. Growth annulations, pittings and deep accidental scars on tube surface (UZM/K.345), x 0.6.

Fig. 3. Siphonal tube fragment (UZM/K.10). Hard (laminated) tube wall enclosing concentric calcite laminations around siphonal canals, exposed by accidental oblique wear, x 1.5.

Fig. 4. Deep impression of a ribbed, subquadrangular bivalve (? genus *Anadara* Gray, 1847) on tube wall (UZM/K.65), x 1.

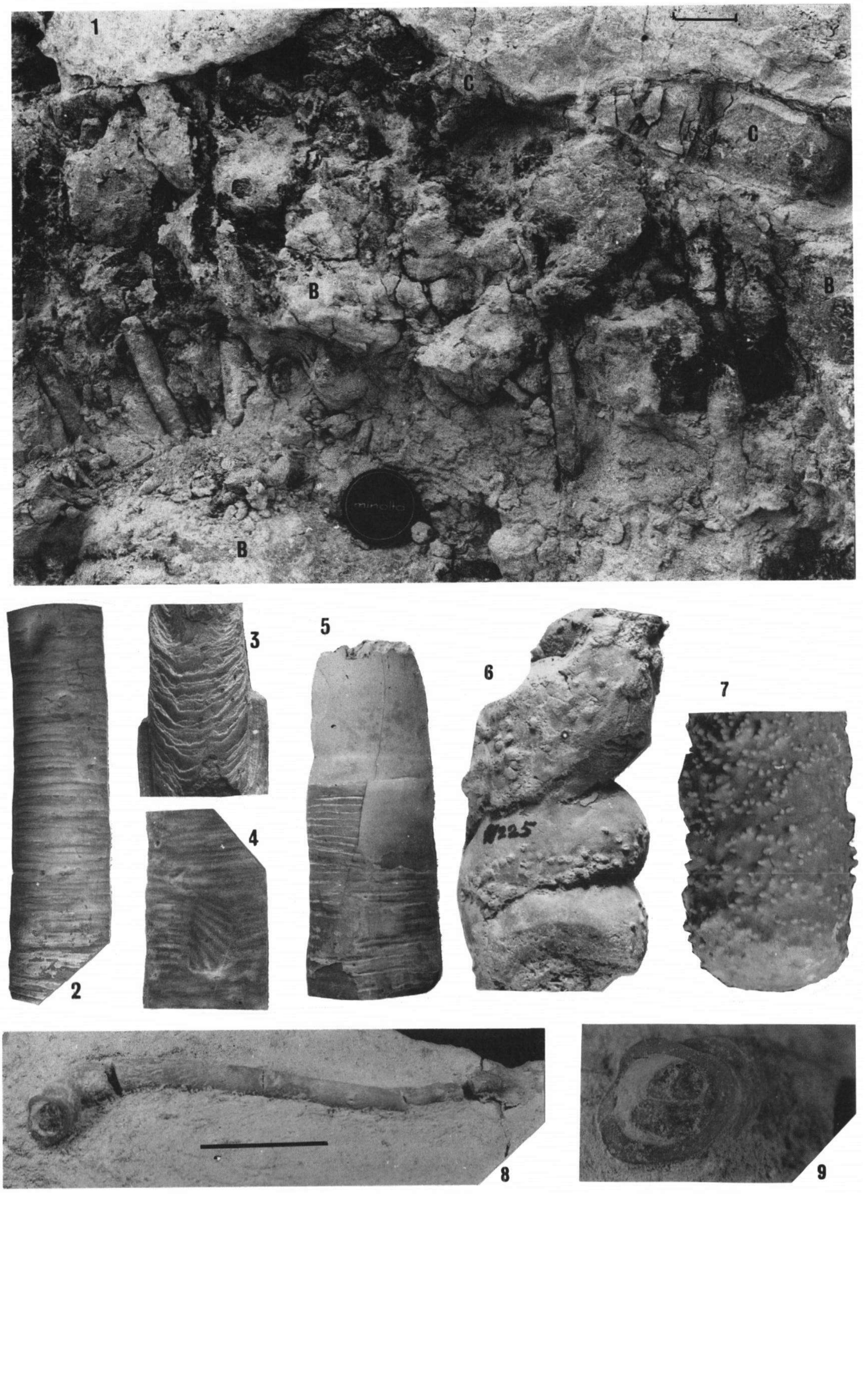
Fig. 5. Annular ridges and coloration of tube are limited to outermost thin laminations (UZM/K.305), x 1.

Fig. 6. Annular swellings of tube UZM/K.225 with calcareous encrustations (compare Pl. 2, Figs 7, 13), x 1.

Fig. 7. Calcareous encrustations on round closed lower (anterior) end of tube (UZM/K.112), x 1.

Fig. 8. A smooth-surfaced, posteriorly-tapering juvenile *Kuphus melitensis* tube (UZM/K.113), with ? evidence of internal division anteriorly. Scale bar equals 1 cm.

Fig. 9. Detail of Fig. 8. Note rounded, externally-undivided, closed, posterior end, x 2.


1
C
C
B
B
minolta
B
2
3
4
5
6
#225
7
8
9

Spratt, T.A.B., 1854. On the Geology of Malta and Gozo, 2nd edition. (The Governor = Wm. Reid) Whitefriars, 16 pp., map.

Tavani, G., 1948. Osservazioni sul genere Kuphus Guettard. — Atti Soc. Tosc. Sci. nat., Mem., (A)55: 1-10, 1 tab.

Tornquist, A., 1904. Über einer eocene Fauna der Westküste von Madagascar. — Abh. Senckenb. naturf. Ges., 27(2): 323-327, pl. 46, fig. 11.

Turner, R.D., 1966. Survey and illustrated catalogue of the Teredinidae (Mollusca: Bivalvia). Cambridge (Museum of Comparative Zoology, Harvard University), vii + 269 pp., 25 figs, 64 pls.

Turner, R.D., 1969. Teredinidae. *In*: R.C. Moore (ed.). Treatise on Invertebrate Paleontology, Part N, Mollusca, Bivalvia, 6(2): N 722-N 741, figs E196-E213. Boulder and Lawrence (The Geological Society of America and University of Kansas Press).

Worm, O., 1655. Museum Wormianum seu Historia rerum rariorum quae Hafniae Danorum in aedibus auctoris servantur. Lugduni Batavorum (Officina Seviriana).

Zammit Maempel, G., 1977. An outline of Maltese geology. Malta (The author), 44 pp., 6 figs, 29 pls.

Zammit Maempel, G., 1979. The Indo-Pacific affinity of some Maltese Tertiary fossils. — Centr. Medit. Nat., 1(1): 1-12.

Zammit Maempel, G., 1982. The earliest 'Treatise' on Maltese fossils. — Melita Historica, 8(2): 133-148.

Zammit Maempel, G., 1989. The folklore of Maltese fossils. — Papers in Mediterranean Social Studies, 1: 29 pp., 4 pls.

Manuscript received 27 February 1993, revised version accepted 8 October 1993.

PLATE 2

Figs 1-10, 12. *Kuphus melitensis* sp. nov. tubes, Late Oligocene, Wied Incita (Malta), except for Fig. 6, which is from the *Kuphus* Beds, Division C, at Attard.

1 - Extrusion of siphons at different levels and subsequent bifurcation of tubes. Thick, lustreless, uneven, calcareous deposit covers emerging siphons (UZM/K.23), x 1.

2 - Siphonal tubes attached proximally, bifurcating distally (UZM/K.24), x 0.7.

3 - Longitudinal section of tube in region of diaphragm, showing section of main undivided tube, diaphragm and internal division without evidence at surface (UZM/K.67), x 1.

4 - Detached, 86 mm long, narrow-bored, tortuous siphonal tube UZM/K.53 with dull and irregular calcite laminations, x 0.9.

5 - Transverse section of tube UZM/K.14 showing incipient formation of second siphonal tube, x 3.5.

6 - Siphonal tube fragment UZM/K.30 with multiple (? post-mortem) *Cliona* sponge borings, x 1.

7 - Longitudinal section of unpartitioned tube fragment UZM/K.210, with dark crystalline layer in its wall showing an almost complete conical internal closure and swelling of tube wall (compare Pl. 1, Fig. 6), x 1.5.

8 - Transverse section of very thick-walled, unpartitioned tube fragment UZM/K.109. Regional thickening of dark crystalline laminations is suggestive of incipient conical internal closure, x 1.5.

9 - Transverse section of siphonal end of tube UZM/K.1, with thick wall, irregularly alternating light and dark coloured laminations and narrow subequal siphonal canals encircled first individually and then jointly (cable-like), x 1.5.

10 - Transverse section of siphonal end of tube UZM/K.300, demonstrating wide, subequal, thin-walled siphonal canals. Narrower siphon about to be extruded, x 2.

12 - Unpartitioned *Kuphus* tube fragment UZM/K.302, with heavy organic calcareous encrustation and perforated conical structures at times interconnected by calcareous filaments, a - exposed tube wall unaffected by the encrustation, x 1.3.

Fig. 11. *Kuphus arenarius* (Linné, 1858), Recent, Ngela Island, Solomon Islands Protectorate. Lowermost segment of tube UZM/KK.1, x 0.4, c - sutures marking site of previous closure of tube; g - deep impression of a turritellid gastropod; o - open lower (anterior) end; p - pittings; r - growth rings; s - deep accidental scars.

Figs 13, 14. *Kuphus* sp. Post-Pliocene beach deposit, South Gaysum Islands, Gulf of Suez, Red Sea. 13 - tube NHML, no. 25131, with calcareous organic encrustations analogous to Pl. 2, Fig. 12, x 1.3; 14 - radiograph of same tube revealing internal closures and camerations, x 1.3.

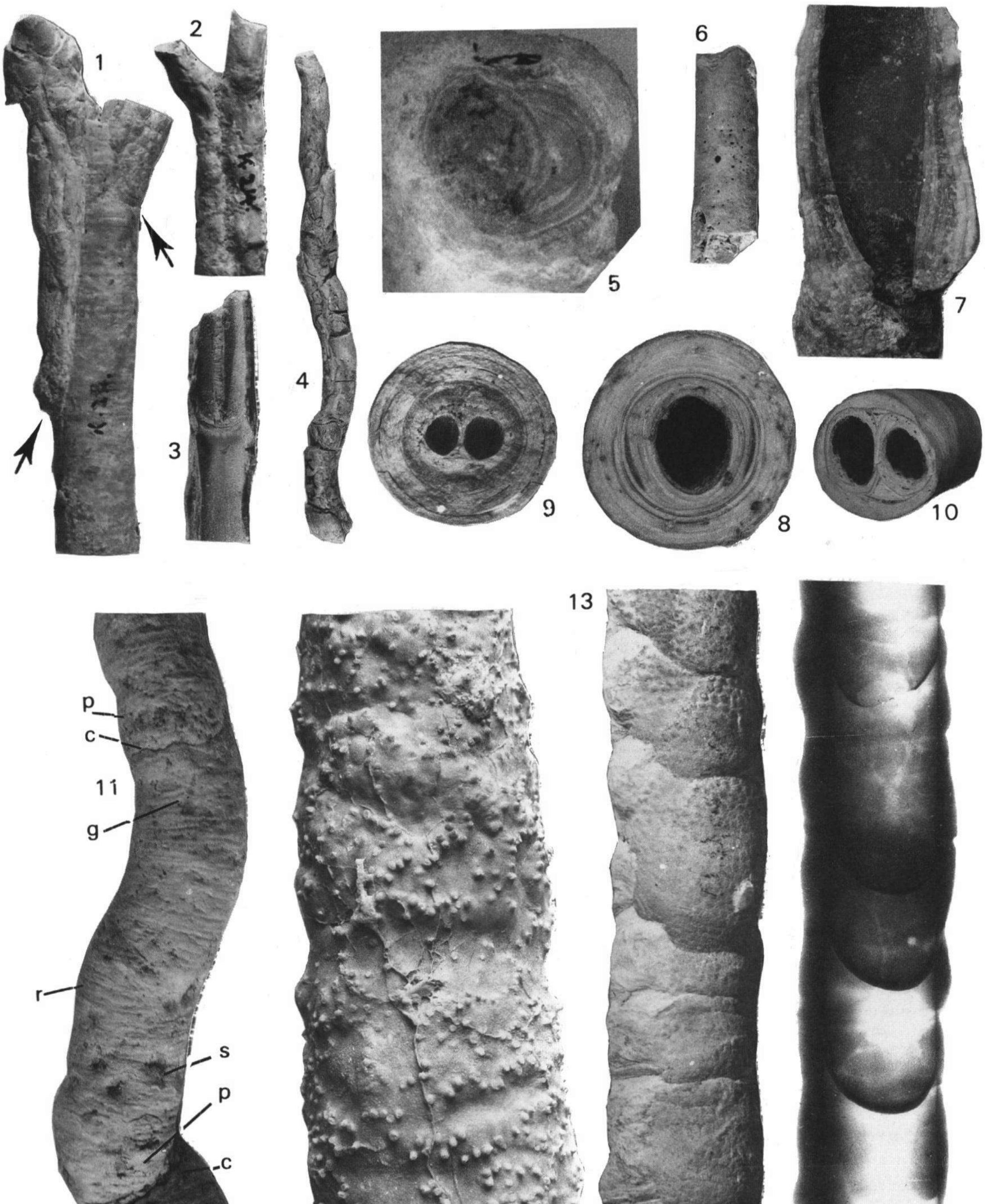

1
2
3
4
5
6
7
9
8
10
p
c
11
g
r
s
p
c
o
12
a
13
14

PLATE 3

Figs 1-4. *Kuphus arenarius* (Linné, 1738), Recent, Solomon Islands.

1 - External view of left pallet (NHML, no. 57.11.30.12), lacking proximal end (handle). Note dorso-ventral curvature of stalk and its extension into the awn dividing cup into a larger (dorsal) and a smaller (ventral) pocket, x 2.

2 - Transverse section of left pallet stalk NHML, no. 1933.7.14.IV, showing laminations around a medial hard core (compare structure of *K. melitensis* pallet, Pl. 3, Fig. 10).

3 - Radiograph of pallet stalk of NHML, no. 1933.7.14.I, showing growth of awn by deposition of horizontal laminations on distal edge.

4 - Anterior view of valves of NHML, no. 1933.7.14.I, in apposition, showing characteristic wide pedal gape, *c* x 2.5.

Figs 5-15. *Kuphus melitensis* sp. nov., *Kuphus* Beds, Lower Coralline Limestone Formation, Attard Member, Late Oligocene, Wied Incita, central Malta.

5, 6 - Tube fragments UZM/K.213 and UZM/K.221, respectively, with both pallets jamming siphonal canals and with handle protruding into unpartitioned tube. Note abnormal development of pallet on left in Fig. 5, x 1.

7 - Crushed tube (UZM/K.212) with both pallets (distal ends slightly chipped) embedded upright in infill of unpartitioned tube section, x 2.

8 - Straight-shafted pallet with an unduly short handle, recovered from an unpartitioned tube fragment (UZM/K.223), Division C of *Kuphus* Beds, Attard, x 2.

9 - Pallet UZM/K.126 with slightly deformed stalk, broken tip and a calcareous development over its handle/stalk junction, x 2.

10 - Detail of upper end of specimen shown in Fig. 9. Note eccentric (medial) hard core as in Recent *Kuphus arenarius* (compare Pl. 3, Fig. 2).

11 - Fragment of internally partitioned tube (UZM/K.215) with partial removal of tube wall to expose a pallet jamming each of the two siphonal canals. Note handles protruding into undivided tube, x 2.2.

12 - Holotype, tube UZM/K.206 with both valves (moulds) embedded in matrix at open end, x 2. Note thickness of valves.

13 - Latex peel from paratype NHML, no. LL.40006 (*ex* Zammit-Maempel Collection, K.106) showing commarginal ornament.

14 - Anterior view of tube UZM/K.48 with internal mould of both valves in apposition, x 1.4.

15 - Rubber peel of internal mould of both valves in apposition in tube RGM 393 033 (UZM/K.203) showing abraded apophysis, x 1.9.