ICHNOLOGICAL NOMENCLATURE OF CLAVATE BORINGS

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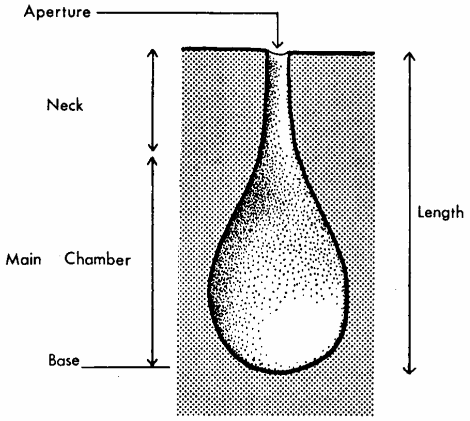
ABSTRACT. The use of ichnoterminology for flask-shaped borings is reviewed. The names *Gastrochaenolites* Leymerie and *Teredolites* Leymerie are recommended for use as ichnogenera for such borings in lithic and lignic substrates respectively. A range of morphology is recognized for each genus and the following new ichnospecies are described: *G. ampullatus*, *G. cluniformis*, *G. dijugus*, *G. lapidicus*, *G. orbicularis*, *G. ornatus*, *G. torpedo*, *G. turbinatus*, and *T. longissimus*. A key is given for rapid identification of the species, and stratigraphic distributions are given.

HITHERTO, there has been no nomenclatural stability in the naming of fossil flask-shaped and club-shaped borings which are common in hardgrounds and in fossil wood. These borings, which are here called clavate (Latin: *clava* = club), are those having usually a single narrow aperture, leading via a narrow neck to a wider chamber within the substrate (text-fig. 1). Such borings are immensely common both today and in the fossil record, and are principally, though not exclusively, the work of bivalves.



TEXT-FIG. 1. Terminology of a clavate boring.

A number of generic names have been used for the borings. The earliest names available are *Gastrochaenolites* and *Teredolites*, both introduced by Leymerie (1842), but they remained rarely used until the late 1960s. Bromley (1972) suggested synonomizing several boring ichnogenera under *Trypanites* but this suggestion did not gain popularity and is now regarded as excessive lumping. Bradshaw (1980) advocated the use of *Teredolites* for all club-shaped borings and redefined the name, but this use is felt here to be still too generalized. Kelly (1980) used *Gastrochaenolites* but later (in Balson 1980), considering that the name was invalid, used *Teredolites*. Other names in current usage may have no status for several reasons: they were not acceptably published, are subjective synonyms of earlier ichnotaxa, are misapplied names of different ichnotaxa, or they bear the names of supposed zoological inhabitants. There are many excellent descriptions of clavate borings, e.g. Raynaud 1969; Evans 1970; Perkins 1971; Andersson 1979. Unfortunately in these cases no ichnotaxa were used.

In the present article the names in general use for clavate borings are examined for availability. The ichnogenera of Leymerie (1842) are found valid and are supplemented with new ichnospecies to name distinctive forms.

CLASSES OF SUBSTRATE

Leymerie (1842) introduced two names for clavate borings: *Gastrochaenolites* for those in lithic substrates, mollusc shell, coral, or limestone and *T. clavatus* for borings in wood. We believe this basic distinction between stony (lithic) and woody (lignic) substrates to be valid and useful. Trace fossils in unconsolidated sediments are named separately from those in hard substrates, e.g. the ichnogenera *Skolithos* and *Trypanites* s.s. and it seems natural to keep such forms separate from those in woody substrates. From the viewpoint of the borer, there are profound physical and ecological differences between stony and woody substrates, differences at least as significant as those between loose sediment and cemented sediment.

In the geological realm, lithic substrates include all indurated rock-types regardless of lithology, as well as hard skeletons such as coral, shell, and bone. In modern terms we must add brickwork, concrete, metal, and plastic. Woody substrates comprise driftwood, mangrove roots, submerged forests, and nut-shells, and today include pilings and ship hulls. Clavate borings occur in all these substrates. There will always be special cases such as how to name clavate borings made in the surface of a coal-seam apparently before it was coalified, but such cases will anyway deserve special description and interpretation, e.g. Bromley *et al.* (1984).

LIBERATED FILLS OF CLAVATE BORINGS

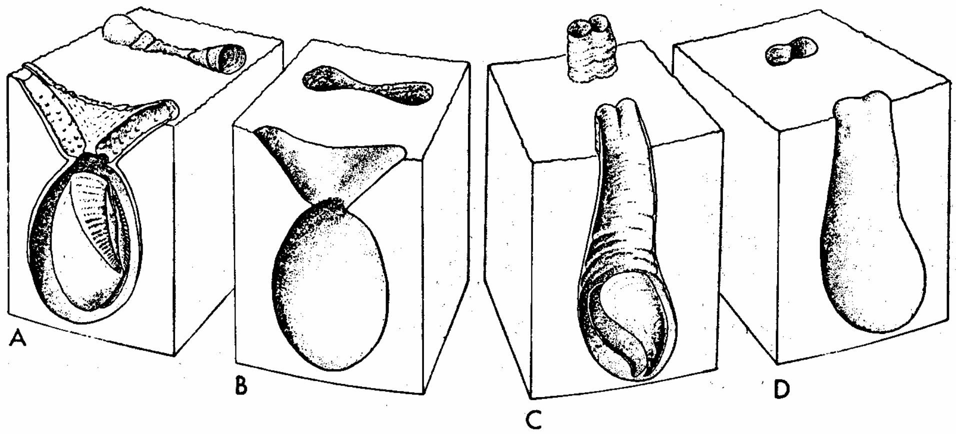
In some sediments, lithified clavate-boring fills occur as loose clasts, having been released by the destruction of their substrate (e.g. Radwanski 1977). This most often occurs in the case of woody substrates where the sediment filling the borings is cemented prior to breakdown of the wood. However, examples are also common where aragonite substrates have been destroyed at the sea floor. In such cases, the original nature of the substrate may not be immediately apparent. However, these borings commonly have a foreign sculptural ornament moulded on the surface which may characterize the vanished substrate, such as grain of wood (e.g. Vitalis 1961) or septal organization of coral (e.g. Damon 1860, p. 79, fig. 35). Also association with other borings that are still preserved in their substrate may provide such evidence. Foreign sculptural ornament can be described as xenoglyphic and should be contrasted with ornament due to direct boring activity such as that caused by the rotating rasping action of pholad bivalves—bioglyphic (terms introduced by Bromley *et al.* 1984).

In cases where there is no indication as to whether the original nature of the substrate was lithic or lignic, an ichnogenus cannot be applied. We anticipate, however, that such cases will be few and will merit individual discussion. They may simply be termed 'clavate-boring infills'.

CARBONATE LININGS IN CLAVATE BORINGS

Many of the organisms that produce clavate borings today, partly or completely line their borings with calcareous deposits. This is particularly the case among boring bivalves (e.g. Savazzi 1982). Some of these produce special linings around the siphonal region at the aperture and neck of the boring, and these deposits may extend as a chimney above the substrate surface (text-fig. 2). The walls of the main chamber may be more or less extensively coated with calcareous deposits, both in lithic and woody substrates. Such linings are commonly well preserved in fossil material.

The mere presence or absence of calcareous linings is of zoo-taxonomic significance; some species are incapable of secreting them, others do so. Among those that do, however, the extent,



TEXT-FIG. 2. A, longitudinal section of *Gastrochaenolites ampullatus* containing the body fossil: based on the boring of *Spengleria rostrata*. B, as A, but as preserved without the body fossil. C, longitudinal section of *G. dijugus* containing the body fossil: based on the boring of *Gastrochaena dubia*. D, as C, but without the body fossil.

morphology, and thickness of the lining is extremely variable from individual to individual. Degree and form of lining vary with ontogeny, substrate structure, crowding of individuals, etc. Furthermore, similar deposits are laid down in some bivalves upon the shells as well as the boring. For these reasons we prefer to regard the lining as part of the hard part of the shell, and to disregard it in ichnotaxonomy.

PREVIOUS NAMES

Gastrochaenolites Leymerie, 1842 and *Teredolites* Leymerie, 1842

In choosing these names, Leymerie was influenced, of course, by his opinion of the nature of the organism responsible for the boring. Thus he added the suffix *-ites*, as was then customary for fossilized material, to the biological taxa *Gastrochaena* and *Teredo*. However, it is clear from Leymerie's text and illustrations that it is the product of the activity of these animals rather than the animals themselves that bear the names, and these names are consequently ichnotaxa. This is a common form of confusion in the erection of early ichnotaxa, cf. *Clionites* Morris 1851, intended for fossil sponge borings (junior synonym of *Entobia* Bronn 1838). While the resulting names are unsatisfactory as ichnotaxa, in implying the work of a single biotaxon, it does not necessarily render the names unavailable, according to the rules of nomenclature. Thus, although *T. clavatus* does not closely resemble the work of *Teredo* spp., the ichnogenus, erected with the type species and well described and illustrated, must be considered available for clavate borings in wood. In contrast, *Gastrochaenolites* was erected without a nominal species, and was regarded by Keen (1968, p. N699) as a *nom. van.* and was placed as a synonym of the body fossil *Gastrochaena*. However, the original description is accompanied by a clear description and illustration and is therefore also valid (R. V. Melville, pers. comm.). Both names suffer from the suggestion of an implied original constructor but this does not affect availability of the names. Zittel (1881, p. 139) placed '*Teredolites* Deshayes' as a synonym of the body fossil *Teredo*. This was followed in the French translation by Barrois (Zittel 1887, p. 138). However, in the English translation by Eastman (Zittel 1900, p. 424, and subsequent edition, 1913, p. 501) it was ascribed correctly to Leymerie. Furthermore, in these translations the ichnotaxon was referred to as 'casts of borings of fossil Teredos'. Vokes (1980) placed *Gastrochaenolites* as *incertae sedis* within the bivalve subfamily Gastrochaenacea, and *Teredolites* as 'subfamily uncertain' within the family Teredinidae. But it must be stressed that *Gastrochaenolites* and *Teredolites* are not body fossils, they are traces of living activity, and cannot be accommodated within a strict zoological systematic nomenclature.

Teredolithus Bartsch, 1930

Bartsch intended this name only as an informal group name (therefore not italicized) for the linings of ship-worm borings of generically unknown status. It was never intended to have generic status and deliberately no type was designated. Turner (*in* Moore 1969: N740–741) used the name at generic level and placed it in 'subfamily uncertain' within the Pholadidae: it is probably only useful in the sense that Bartsch originally intended and, since we regard linings as related to the hard parts of fossils, we do not consider the name to be an available ichnogenus.

Trypanites Mägdefrau, 1932

The type ichnospecies, *T. weisei* Mägdefrau is a simple cylindrical boring having a single aperture. The apparent lack of a name for clavate borings led Bromley (1972) to suggest extending this ichnogenus to cover a wider range of single entrance borings, including clavate forms. However, this solution has not been generally accepted, and it would seem preferable to restrict *Trypanites* to cylindrical, commonly meandering, or convoluted borings.

Martesites Vitalis, 1961

This name refers to clavate borings in wood having a circular cross-section, and is a junior synonym of *Teredolites* Leymerie. Vokes (1980) regarded this as a body fossil placing it as a genus within the family Pholadidae Lamarck.

Paleolithophaga Chiplonkar and Ghare, 1967

This name was introduced as an ichnogenus with type species *P. andurensis* Chiplonkar and Ghare (1976, p. 162), to cover 'all the fossil borings of chemically-boring bivalves'. The diagnosis describes the borings as circular, having diameters from 0·7 to 1·0 cm and depths up to 2·0 cm. The only material is a single block of limestone containing many pits of varying morphology. No holotype was designated. It is a junior synonym of *Gastrochaenolites*.

Lithophaga, *Teredo*, etc.

In the absence of an ichnotaxon, a common procedure has been to apply the name of the *supposed* borer to the boring itself. Since, in the case of many borings, direct evidence of the nature of the borer is lacking, this is a most unsatisfactory solution to the problem (Bromley and Fürsich 1980; Bromley 1981).

SYSTEMATIC ICHNOLOGY

Key to identification of ichnospecies of *Gastrochaenolites* and *Teredolites*

1.	Substrate lithic	2
	Substrate lignic	10
2.	Boring circular throughout length	3
	Boring bilaterally symmetrical (apart from axial twists)	6
3.	Boring having near spherical main chamber	*G. orbicularis*
	Boring having elongate main chamber	4
4.	Base of main chamber having concentrically/spirally grooved bioglyph	*G. ornatus*
	Base of boring smooth	5
5.	Boring moderately elongate, widest at mid-length	*G. lapidicus*
	Boring elongate, widest at base	*G. turbinatus*

6.	Neck region of two tubes either connected or separate	7
	Neck region a single tube, may be compressed	8
7.	Neck consisting of two separate diverging tubes or connecting slot	*G. ampullatus*
	Neck with two parallel conjoined tubes	*G. dijugus*
8.	Base of boring bilobed	*G. cluniformis*
	Base of boring smooth	9
9.	Base of boring bluntly parabolic	*G. lapidicus*
	Base of boring acutely parabolic	*G. torpedo*
10.	Moderately elongate, substrate grain mainly perpendicular to axis of boring	*T. clavatus*
	Very elongate, substrate grain mainly parallel to axis of boring	*T. longissimus*

The systematic annotation of Richter (1948), described in English by Matthews (1973), is followed here.

Ichnogenus *Gastrochaenolites* Leymerie, 1842

*. 1842 *Gastrochaenolites* Leymerie.
p. 1972 *Trypanites* Mägdefrau; Bromley.
. 1976 *Paleolithophaga* Chiplonkar and Ghare.
. 1980 *Teredolites* Leymerie; Bradshaw.
. 1980 *Gastrochaenolites* Leymerie; Kelly.
. *1980* *Teredolites* Leymerie; Kelly (*in* Balson 1980).

Type species. G. lapidicus ichnosp. nov.

Diagnosis. Clavate borings in lithic substrates. The apertural region of the boring is narrower than the main chamber and may be circular, oval, or dumb-bell shaped. The aperture may be separated from the main chamber by a neck region which in some cases may be widely flared. The main chamber may vary from subspherical to elongate, having a parabolic to rounded truncated base and a circular to oval cross section, modified in some forms by a longitudinal ridge or grooves to produce an almond- or heart-shaped section. The general range in morphology of species of *Gastrochaenolites* is shown in text-fig. 3A–H.

Remarks. The axis of the boring may be straight, curved, or irregular. The widest part is usually between the mid-point and the base of the boring. The surface of the boring may be smooth, or bear sculptural ornament. The ornament may derive from the physical boring process, in which case, among bivalves, it may reflect the sculpture of the shells of the constructor (i.e. bioglyph); or it may derive from structural heterogeneity of the substrate (i.e. xenoglyph). The xenoglyph has no ichnotaxonomic significance at species level. Typical *Gastrochaenolites* range in size of diameter from 2 to 45 mm, and in length from 3 to 100 mm.

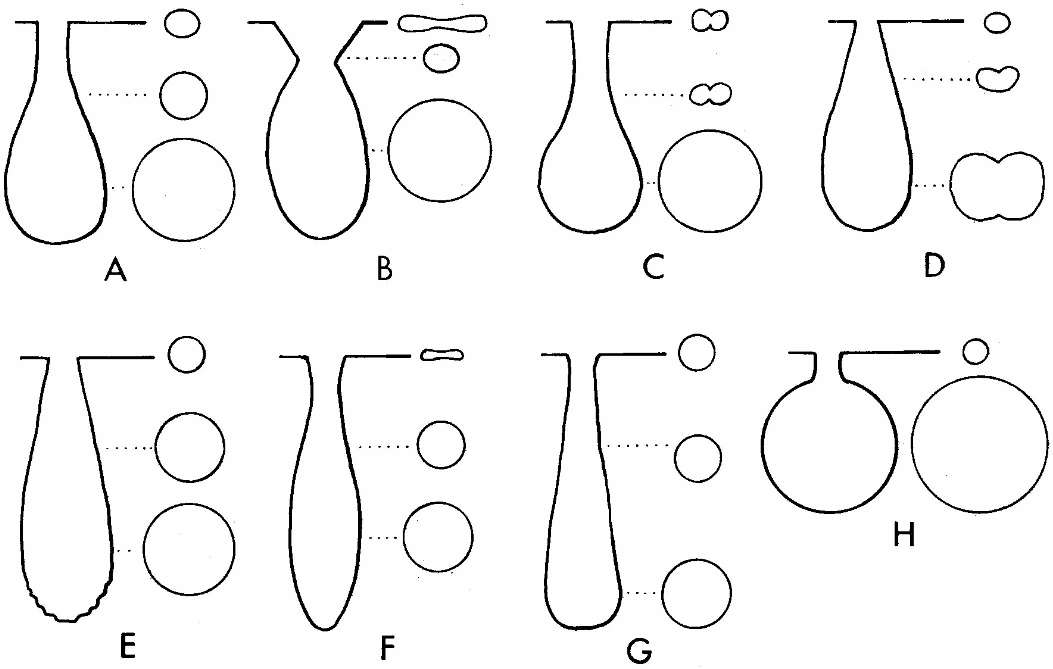
The constriction in the apertural/neck region immediately distinguishes it from *Trypanites* Mägdefrau. *Rogerella* Saint-Seine 1951, *Zapfella* Saint-Seine 1956, *Brachyzapfes* Codez and Saint-Seine 1958, and *Simonizapfes* Codez and Saint-Seine 1958 are all small oblique sac-like borings having a tendency towards a narrow tear-shaped slit aperture. They are attributed to acrothoracic barnacles. Borings of the polychaete *Polydora* have twin tube apertures, but there is no distinct chamber, the boring being a modified 'U' tube shape. The U-borings of the ichnogenus *Caulostrepsis* are morphologically distinct, lacking a main chamber (Bromley and D'Alessandro 1983).

Range. Jurassic to Recent.

Gastrochaenolites lapidicus ichnosp. nov.

Text-figs. 3A, 4A–B

. 1842 *Gastrochaenolites* Leymerie, p. 2, pl. 3, fig. 1*a–c*.
v. 1980 *Gastrochaenolites* Leymerie; Kelly, p. 771, text-figs. 2A–G, 3A–D, pl. 96, figs. 17–20, 22–24.
v. *1980* *Teredolites* Leymerie; Kelly in Balson, p. 726.



TEXT-FIG. 3. Sketches of range in morphology of species of *Gastrochaenolites*, showing cross-sectional shape at various levels within the borings. A, *G. lapidicus*; B, *G. ampullatus*; C, *G. dijugus*; D, *G. cluniformis*; E, *G. ornatus*; F, *G. torpedo*; G, *G. turbinatus*; H, *G. orbicularis*.

In addition numerous references have been made to the boring with varying degrees of anonymity, e.g. Andersson (1979, type 3, p. 6, fig. 6C).

Holotype. British Geological Survey, Kelly Collection, Zu2230, from the Basal Spilsby Nodule Bed, Spilsby Sandstone, Middle Volgian; Nettleton, Lincolnshire, England. Figured originally by Kelly (1980, 771, fig. 2B).

Derivatio nominis. Latin, *lapidicus* = stonecutter.

Diagnosis. Smooth, clavate boring; elongate ovate; circular cross-section throughout length including the neck region except for the immediate area of the aperture where the section is usually oval, but may be circular; base bluntly paraboloid in longitudinal section; widest diameter located approximately central within the main chamber.

Remarks. There is a clear neck region which is a distinguishing feature separating it from *G. turbinatus*. Borings of this type are produced by several species of *Lithophaga* and *Hiatella* today, the former commonly lined but the lining never extending significantly beyond the aperture.

Range. Jurassic to Recent (pre-Jurassic *Lithophaga* probably had a nestling habit and are not yet known to have bored).

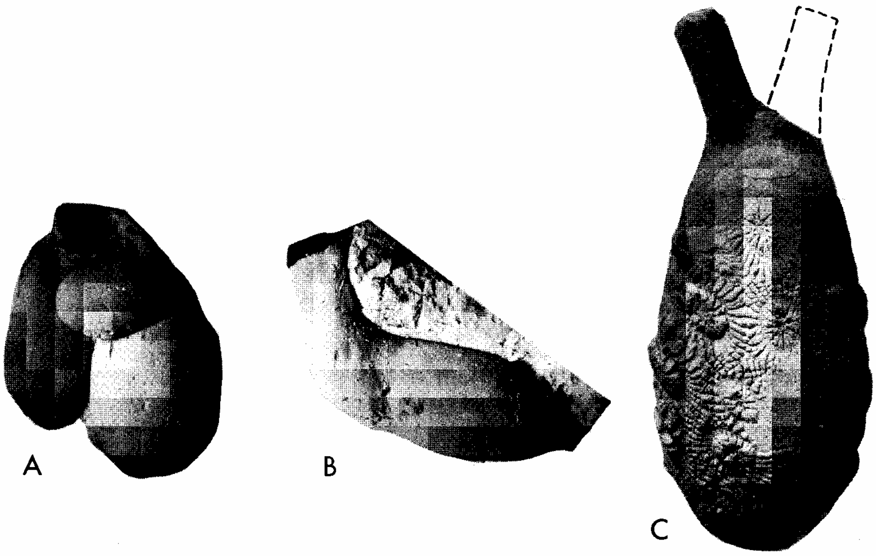
Gastrochaenolites ampullatus ichnosp. nov.

Text-figs. 2A–B, 3B, 4C

Holotype. BM(NH) 15174, Last Collection, Tertiary (Neogene) 40 ft from surface; Mbweni, Zanzibar (one apertural tube damaged).

Derivatio nominis. Latin, *ampulla* = small globular flask or bottle with two handles.

Diagnosis. Smooth borings with outline of main chamber spherical to elongate but having a fan-shaped, flared neck and containing two diverging tubes leading to twin apertures; maximum diameter near centre of main chamber.



TEXT-FIG. 4A, B. *Gastrochaenolites lapidicus* ichnosp. nov. A, interpenetrating paratypes, BGS Kelly Collection Zn2232; B, holotype, same collection, Zu2230; both from Basal Spilsby Nodule Bed, Middle Volgian; Sand Pit, 200 m south-east of Top Barn, Nettleton, Lincolnshire. Phosphatic nodule substrate, × 1·5. C, *G. ampullatus* ichnosp. nov. holotype, BM(NH) L15174, Last Collection, Tertiary (Neogene), 40 ft from surface; Mbweni, Zanzibar. One apertural tube damaged. Coral substrate, × 1.

Remarks. The flared neck distinguishes *G. ampullatus* from other species. The main chamber may range from subspherical to elongate. The neck is thickly lined to produce two diverging siphonal tubes. The structure of the lining is complex, having arisen through migration of tubes with the growth of the animal (see text-fig. 2A–B). A common mode of preservation is shown in text-fig. 4C, where the fill was cemented prior to the loss of the lining, producing a combination mould of body fossil and boring. In these cases the true form of the neck is obscured. Borings of this type are produced today by *Spengleria rostrata* (Warme 1975, fig. 11.26; Bromley 1978, fig. 9 left).

Range. Neogene to Recent.

Gastrochaenolites cluniformis ichnosp. nov.

Text-figs. 3D, 5

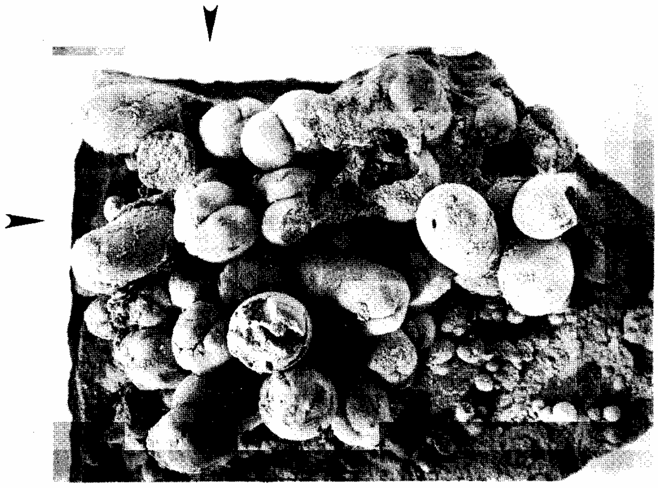
Holotype. BM(NH) L21602, Hythe Beds, Lower Greensand, Aptian; Maidstone, Kent.

Derivatio nominis. Latin, *cluniformis* = buttock shaped.

Diagnosis. Smooth *Gastrochaenolites* having one principal ridge in the main chamber and a second weakly developed one diametrically opposite. The base is rounded to bilobate. The neck and aperture are rounded to oval.

Remarks. The principal ridge and bilobate form distinguish *G. cluniformis* from *G. dijugus*. Borings of this type are found in corals and are produced by *Botula* spp.

Range. Cretaceous to Recent.



TEXT-FIG. 5. *Gastrochaenolites cluniformis* ichnosp. nov. Assemblage with holotype arrowed. BM(NH) L21602, Hythe Beds, Lower Greensand, Aptian, Cretaceous; Maidstone, Kent. Lithic substrate, ×1.

Gastrochaenolites dijugus ichnosp. nov.

Text-figs. 2C–D, 3C, 6A–B

. 1980 *Teredolites clavatus* Leymerie; Bradshaw, p. 290, text-figs. A–E.

Holotype. BM(NH) L36922, Corallian, Oxfordian, Jurassic; Calne, Wiltshire, England; paratype, BM(NH) L71398, same horizon, Malton, Yorkshire, England.

Derivatio nominis. Latin, *dijugus* = having two ridges.

Diagnosis. Smooth *Gastrochaenolites* in which neck region is constricted in the form approaching a figure of eight by two opposed ridges.

Remarks. The boring is commonly lined in the neck region, the lining usually continuing above the surface as a fused pair of extension tubes. *Gastrochaena* is a known occupant from Jurassic to Recent; the carinate *Gastrochaenopsis* is also known from the Jurassic only.

Range. Jurassic to Recent.

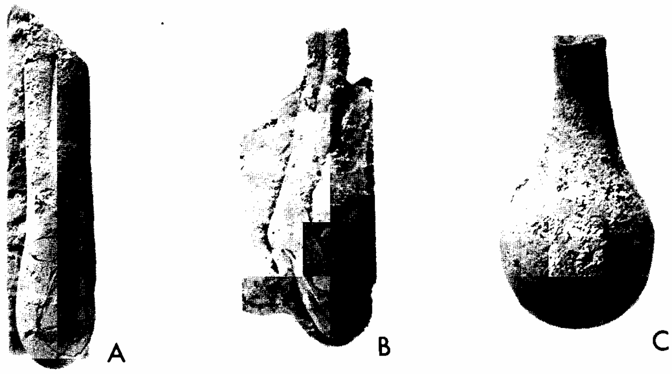
Gastrochaenolites orbicularis ichnosp. nov.

Text-figs. 3H, 6C

Holotype. BM(NH) L8138, Damon Collection, mid-Cenomanian to early Turonian; Tourtia de Tournai, Belgium.

Derivatio nominis. Latin, *orbis* = orb.

Diagnosis. Smooth *Gastrochaenolites*, circular in cross-section throughout; main chamber orbicular; neck region elongate in type specimen but may be short.



TEXT-FIG. 6A, B. *Gastrochaenolites dijugus* ichnosp. nov. A, paratype, BM(NH) L71398 Corallian, Oxfordian; Malton, Yorkshire, England. Coral substrate, ×1; B, holotype, BM(NH) L36922, Corallian, Oxfordian, Jurassic, Calne, Wiltshire. Coral substrate, ×1. C, *G. orbicularis* ichnosp. nov. holotype, BM(NH) L8138, Damon Collection, mid-Cenomanian–early Turonian, Cretaceous; Tourtia de Tournai, Belgium. Lithic substrate, ×1.

Remarks. The orbicular main chamber and circular cross-section to the neck distinguish this species from others. Borings of this type are produced by *Jouannetia*. There may be an inconspicuous thin lining.

Range. Jurassic to Recent.

Gastrochaenolites ornatus ichnosp. nov.

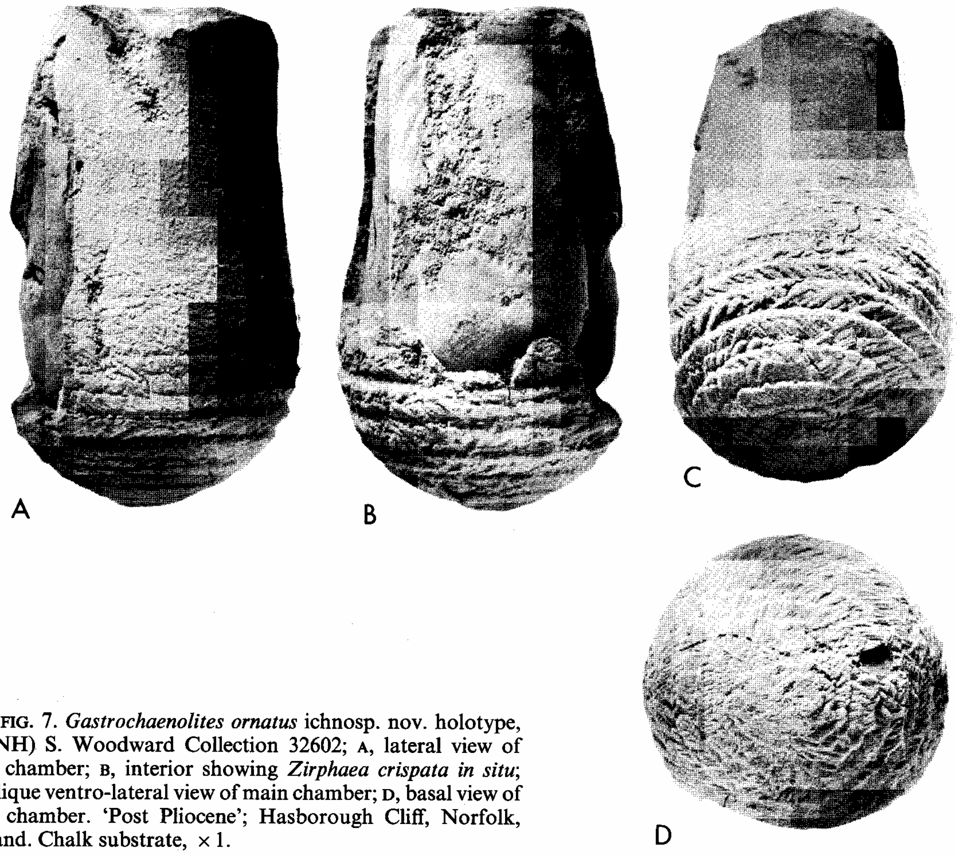
Text-figs. 3E, 7A–D

Holotype. BM(NH) S. Woodward Collection 32602. Originally figured S. Woodward (1833, p. 39, pl. 1, fig. 19) as: 'Pholas crispata; *auctor*. Imbedded in a pyritous cast of the cavity formed by the animal in the rock.' Post-Pliocene, from Hasborough Cliff, Norfolk, England.

Derivatio nominis. Latin, ornatus = ornamented.

Diagnosis. *Gastrochaenolites* that are circular in cross-section throughout. Deepest portion bears circular or spiral bioglyph, sometimes serrated grooves.

Remarks. These are unlined borings commonly found in association with pholad bivalves. The holotype contains the remains of *Zirfaea crispata*. The concentric grooves were formed by the serrated anterior portion of the shell rotating within the boring and grinding away the base of the boring, thus enlarging it. Although bioglyphic ornament may be present on other ichnospecies of *Gastrochaenolites*, the present form has such strongly developed bioglyph that it deserves distinction as a separate ichnospecies. The morphology otherwise resembles that of *G. turbinatus*. Warme and McHuron (1968) figure *Jouannetia* associated with such borings; Röder (1977, p. 136, fig. 15) figures



TEXT-FIG. 7. *Gastrochaenolites ornatus* ichnosp. nov. holotype, BM(NH) S. Woodward Collection 32602; A, lateral view of main chamber; B, interior showing *Zirphaea crispata in situ*; C, oblique ventro-lateral view of main chamber; D, basal view of main chamber. 'Post Pliocene'; Hasborough Cliff, Norfolk, England. Chalk substrate, × 1.

Recent *Barnea* in association with these borings and (1977, pl. 3) figures Recent borings of this type which were constructed by *Pholas*.

Range. Pleistocene to Recent.

Gastrochaenolites torpedo ichnosp. nov.

Text-figs. 3F, 8A–B

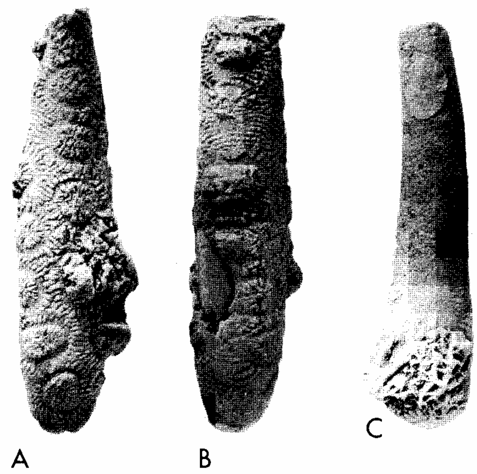
Holotype. BM(NH) 56735, labelled Pliocene, but probably Jaffna Limestone, L. Miocene (Cooray 1967, 135; 1982); Kankesanturai, north of Jaffna, Sri Lanka.

Derivatio nominis. Named after its similarity to the weapon.

Diagnosis. Elongate smooth boring, widest point close to mid-line with the base acutely parabolic. The neck region is markedly compressed but the aperture itself is oval or approaches a figure-of-eight shape.

Remarks. Differs from *G. lapidicus* by having a more elongate shape and a more compressed neck region. The borings are commonly lined. The lining thins towards the widest part of the boring and may have a transverse wrinkled ornament internally. The lining thickens towards the aperture where the lumen of the boring is restricted to a figure-of-eight cross-section, and continues beyond the substrate surface as a chimney. Borings of this type are constructed today by some species of *Gastrochaena* (cf. Bromley 1978, fig. 9 right) and also of *Lithophaga*. Certain borings of polychaetes and sipunculids resemble this ichnospecies (See Bromley, 1970, p. 63, figs. 4*b*, 4*c* respectively), but are generally more slender.

Range. Jurassic to Recent.



TEXT-FIG. 8. *Gastrochaenolites torpedo* ichnosp. nov. A, B, holotype, BM(NH) 56735, two views of holotype, probably Jaffna Limestone, lower Miocene; Kankesanturai, north of Jaffna, Sri Lanka. Coral substrate, × 1. C, *G. turbinatus* ichnosp. nov. holotype, BM(NH) L56724, probably Jaffna Limestone, lower Miocene; Kankesanturai, north of Jaffna, Sri Lanka. Coral substrate, × 1.

Gastrochaenolites turbinatus ichnosp. nov.

Text-figs. 3G, 8C

Holotype. BM(NH) L56724, labelled Pliocene, but probably Jaffna Limestone, L. Miocene (Cooray 1967, 135; 1982); Kankesanturai, north of Jaffna, Sri Lanka.

Derivatio nominis. Latin, *turbinatus* = conical.

Diagnosis. Smooth *Gastrochaenolites*, acutely conical, having evenly tapered body and neck, the widest point close to the short rounded base; rounded cross-section throughout length.

Remarks. Distinguished from other ichnospecies of *Gastrochaenolites* by the evenly tapered main chamber which merges imperceptibly with the neck. No known linings. Holotype bears some traces of a coral substrate. *Gastrochaena* sp. has been seen occupying Jurassic examples. *Penitella* forms such borings in Recent examples (e.g. Warme 1970, pl. 4).

Range. Jurassic to Recent.

Ichnogenus *Teredolites* Leymerie, 1842

1841 *Teredolites* Leymerie, p. 341 (*nom. nud.*).
*. 1842 *Teredolites* Leymerie, p. 2, pl. 2, figs. 4, 5.
1852 *Teredolithes* Herrmannsen, p. 131 (*nom. nud.*).
. 1900 *Teredolites* Leymerie; Zittel, p. 424, fig. 787D.
. 1913 *Teredolites* Leymerie; Zittel, p. 501, fig. 336D.
. 1961 *Martesites* Vitalis, p. 124, pls. 1-2.

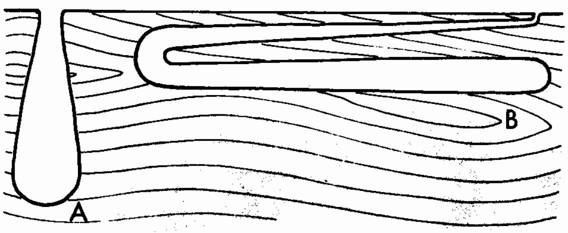
p1972 *Trypanites* Mägdefrau; Bromley, fig. 1B, E only.
1972 *Teredolites* Leymerie; Hatai and Murata, p. 7, pl. 1.
1975 *Martesites* Vitalis; Häntschel, W129.
1975 *Teredolites* Leymerie; Häntschel, W135.
v *non* 1981 *Teredolites* Leymerie; Kelly *in* Balson 1981, p. 726.

Type species. T. clavatus Leymerie 1842 (see below).

Diagnosis. Clavate borings in woody substrates, acutely turbinate, evenly tapered from aperture to base of main chamber; neck region not separated from main chamber; cross-sections at all levels more or less circular; elongate to short.

Remarks. Borings are normally smooth, but may bear the xenoglyph of the grain of the lignic substrate. Faint bioglyphic ornament may also be preserved (Bromley *et al.* 1984). Axis of boring may be straight, sinuous, or contorted. The axis of the boring may change suddenly and cause a constriction in the pattern of the tube (Röder 1977, p. 147, fig. 21). Linings of these borings, as body fossils, fall within the group name Teredolithus Bartsch. Typical species are shown in text-fig. 9.

Range. Jurassic to Recent.



TEXT-FIG. 9. Range in morphology of *Teredolites*. A, *T. clavatus* Leymerie; B, *T. longissimus* ichnosp. nov., both generalized axial sections showing relationship to grain of lignic substrate. Cross-sectional shape round throughout length, × 1.

Teredolites clavatus Leymerie, 1842

Text-figs. 9A, 10

. *1841* *Teredolites clavatus* Leymerie, p. 341 (*nom. nud.*).
*. 1842 *Teredolites clavatus* Leymerie, p. 2, pl. 2, figs. 4, 5.
. 1961 *Martesites vadaszi* Vitalis, p. 124, pl. 1, 2.
. 1969 *Teredolites clavatus* Leymerie; Turner (*in* Moore, ed.), p. N740, fig. 214, 2*a*, *b*.
. 1972 *Trypanites vadaszi* (Vitalis); Bromley, fig. 1B.
. 1975 *Martesites vadaszi* Vitalis; Häntzschel, p. W129, fig. W79, 1.
v. *1983* *Teredolites*; Kelly and Rawson, p. 70.
v. *1983* *Teredolites*; Kelly, p. 287.
v. 1984 *Teredolites clavatus* Leymerie; Bromley, Pemberton and Rahmani, p. 488.

Type specimen: Untraced, Leymerie Collection, Calcaire à Spatangues, Hauterivian, lower Cretaceous, Aube, France.

Diagnosis. Clavate *Teredolites* predominantly perpendicular to the grain in woody substrates having length/width ratio usually less than 5.

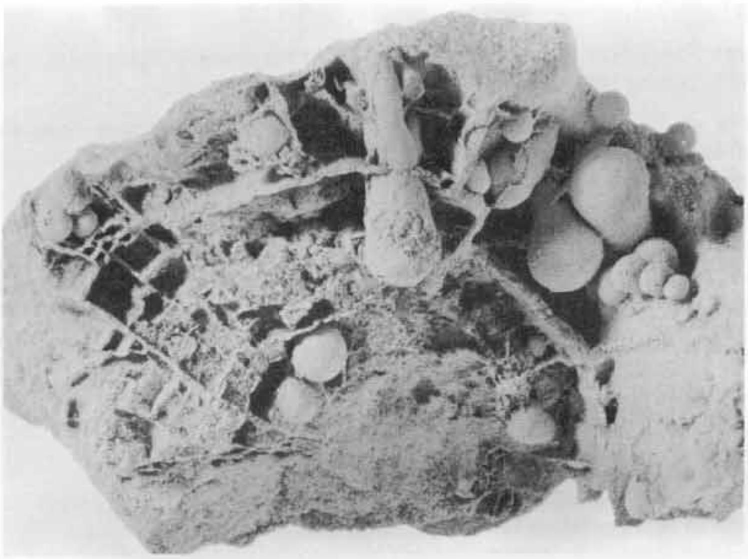
Remarks. Such borings are produced today by species of *Martesia*. Fossil occupants include *Martesia* and *Opertochasma*.

Range. Jurassic to Recent.

Teredolites longissimus ichnosp. nov.

Text-figs. 9B, 11A–B

Holotype. BM(NH) Bensted Collection, 38019, Kentish Rag, Aptian, Lower Cretaceous, Hythe, Kent, England.



TEXT-FIG. 10. *Teredolites clavatus* Leymerie. SMC B11389, Spilsby Sandstone, probably Ryazanian; Benniworth Haven (probably the Railway Cutting south-west of Donington-on-Bain), Lincolnshire. Borings perpendicular to surface of log of wood, ×2.

TEXT-FIG. 11. *Teredolites longissimus* ichnosp. nov. Lateral views (A and B) of holotype (arrowed), with paratypes, BM(NH) Bensted Collection 38019, Kentish Rag, Aptian, lower Cretaceous; Hythe, Kent, England. Borings parallel to grain of lignic substrate, ×1.

Derivatio nominis. Latin, *longissimus* = longest.

Diagnosis. Clavate *Teredolites* predominantly parallel to the grain in lignic substrate having length/width ratio usually greater than 5. Commonly sinuous to contorted.

Remarks. Commonly lined with calcite, the thickness of which increases towards the aperture. Borings of the teredine ship-worms which include those of *Teredo* itself, fall within this ichnospecies. Juvenile forms pass through a phase having the morphology of *T. clavatus*.

Range. Cretaceous to Recent.

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