

# JUVENILE GASTROPODS FROM THE UPPER DEVONIAN CEPHALOPOD BEDS AND ADJACENT STRATA OF CENTRAL IRAN

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## Abstract

Microgastropod fauna from the Upper Devonian Cephalopod Bed and overlying Lower Tournaisian strata of the original reference section of the Shishtu Formation have been examined. Twenty genera and one unknown genus have been identified. The original aragonite shells have been replaced either by pyrite or fluorapatite.

## Introduction

The studied sections are located in the Howz-e-Dorah area in the southern part of the Shotori Range, Central Iran (Fig. 1). Whilst undertaking research on conodont-bearing sections in Central and Northern Iran [1], the discovery was made of a section which yielded an interesting and diverse juvenile gastropod fauna from acid residues. This enables the juvenile stages of many Late Devonian and Early Carboniferous gastropod genera to be illustrated and described. Despite the rich microgastropod fauna, gastropods have not been recorded in previous work.

The gastropod faunas have been extracted from residues of the upper part of Shishtu 1 and lower part of Shishtu 2 subformations in a sequence of 100 metres thick (Figs. 2 and 3). Samples were processed by formic acid, picked by hand and the residues were searched for all organic remains.

Almost all specimens are less than 1 mm in size. Generally, fossils are grey to dark grey in colour, except those from the Cephalopod Bed which are light brown (sample G. 10) or dark red (samples G. 3, G. 4 and G. 8). Most of the specimens show a smooth surface without any ornamentation, but a limited number show some simple ornamentation. Generally, the whole shell of specimens is preserved apart from the aperture which in most of the specimens is not seen.

**Keywords:** Cephalopod bed; Central Iran; Gastropods; Upper Devonian

Samples G. 7 and G. 8 produced very rich fauna and samples G. 1 and G. 5 yielded rich fauna.

XRD and SEM analysis showed that the original aragonite compositions of the gastropoda shells have been replaced either by pyrite or fluorapatite (Figs. 4 and 5). Pyrite specimens come from the Cephalopod Bed and fluorapatite shells from the sequence overlaying the Cephalopod Bed. The illustrated materials are held by the author in the Department of Geology, University of Mashhad.

## Stratigraphy

The studied fauna was yielded from strata which form part of the reference section of Shishtu Formation explained by Stocklin *et al.* [12]. This section is located at Howz-e-Dorah in the southern part of the Shotori Range, Central Iran. The type locality of the Shishtu Formation is situated in the Ozbak-Kuh Mountains [Ruttner *et al.* unpublished] about 120 km to the north of the reference section.

An age of Upper Devonian to Lower Carboniferous is given for the Shishtu Formation [12] which is subdivided into two subformations: Shishtu 1 and Shishtu 2. Each subformation contains goniatite levels called Goniatite Horizons 1 and 2 respectively. According to Stepanov [11], the age of Shishtu 1 is Frasnian and Famennian, probably including Early Tournaisian, and Shishtu 2 is dated as Late Tournaisian to Early Viséan. The equivalent of the

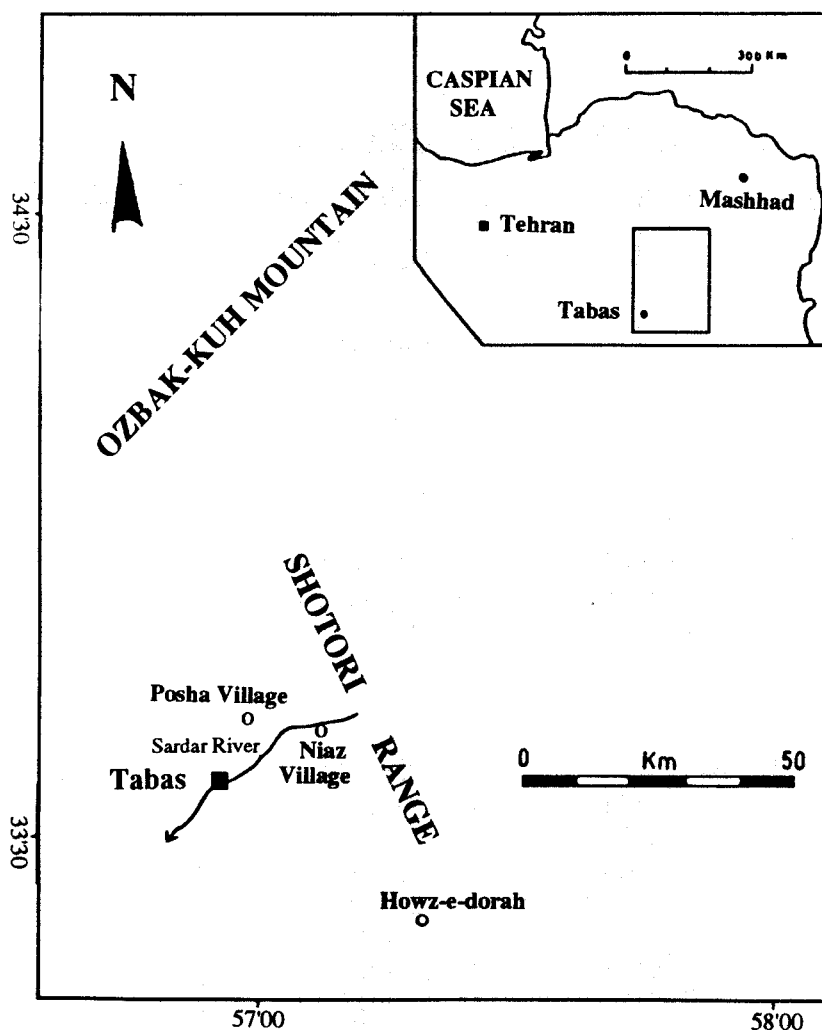


Figure 1. Map of the studied area.

Goniatile Horizon 1 in the reference section has been called Cephalopod Bed [12].

The lower part of the studied section contains the upper part of Shishtu 1 Subformation, with a thickness of 326 metres, and consists of dark-green shale, interbedded with quartzite and sandstone. The sequence contains intercalations of fossiliferous shale, sandstone, oolitic limestone and iron-oolite, which includes the Cephalopod Beds. The Cephalopod Bed is represented by rich fauna exposed across the western foot of the Shotori Range for a distance of 70 km. Towards the north, around Niaz village, on both sides of the Sardar River, and as well as the last exposure around Posha village, an extremely rich fauna has been recorded which includes cephalopods, corals, bryozoans, crinoids and brachiopods [12]. The upper part of the studied section consists of the lower part of the Shishtu 2 Subformation.

A conodont study of Devonian and Carboniferous of Iran [1] includes the present reference sections. The author has correlated previous research on the Shishtu Formation reference section with his conodont results.

### Systematic Palaeontology

In total twenty genera have been identified in one of which (*Loxonema*) three different forms have been introduced. Furthermore, one specimen was introduced whose systematic relation is not known. The familial classification used in the treatise is followed herein.

Letters A, C, H, W, P and S have been used as abbreviations for apertural height, conical angle, shell height, shell width, pleural angle and sutural angle respectively. All age assignments given herein are based on Ashouri [1].

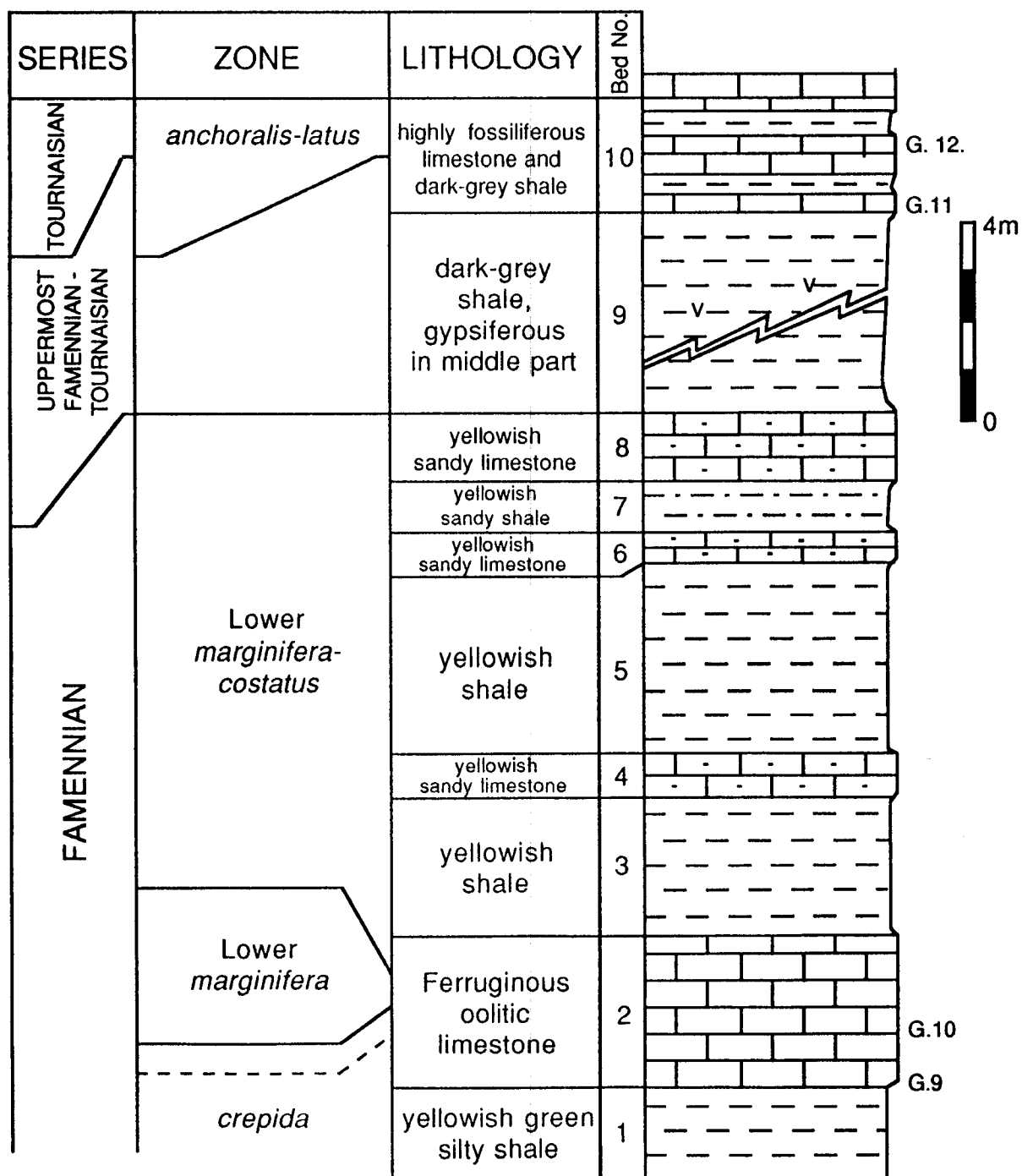


Figure 2. Reference section of part of the Cephalopod Bed and overlying strata in the Howz-e-Dorah area (Section A).

Subclass Prosobranchia MILNE EDWARDS, 1848  
Order Archaeogastropoda THIELE, 1925  
Suborder Bellerophontina ULRICH & SCOFIELD, 1897

Superfamily Bellerophontacea M'COY, 1851  
Family Bellerophontidae M'COY, 1851  
Subfamily Carinaropsinae ULRICH & SCOFIELD, 1897

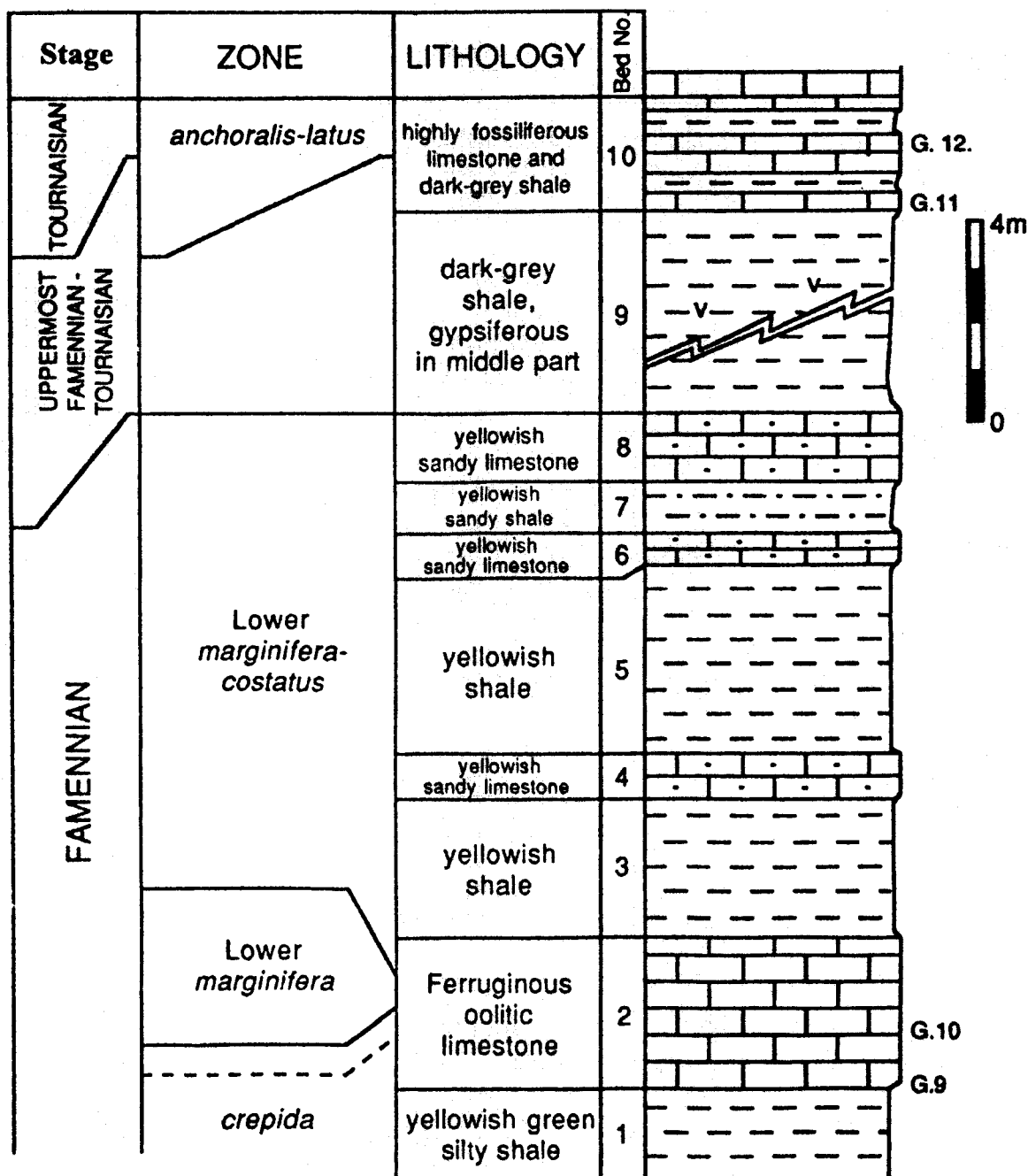


Figure 3. Reference section of part of the Cephalopod Bed and overlying strata in the Howz-e-Dorah area (Section B).

Genus *Bucanopsis* ULRICH, IN ULRICH & SCOFIELD, 1897

Plate 1, Figure 1

#### Description

Shell isostrophic, nautiliconic, almost globose or rounded with tendency to rapid expansion of whorls;

suture deep, acute, umbilici deeply and equally concave rather broadly open, showing the margins of the interior whorls; whorls rising from the suture in an inward curve, and then rounding rapidly over the sides to the back, which is rather broad and flatly convex. Ornament of rather regular growth lines is displayed in the last 3/4 of the last whorl (the last 1/4 of last whorl is not preserved).

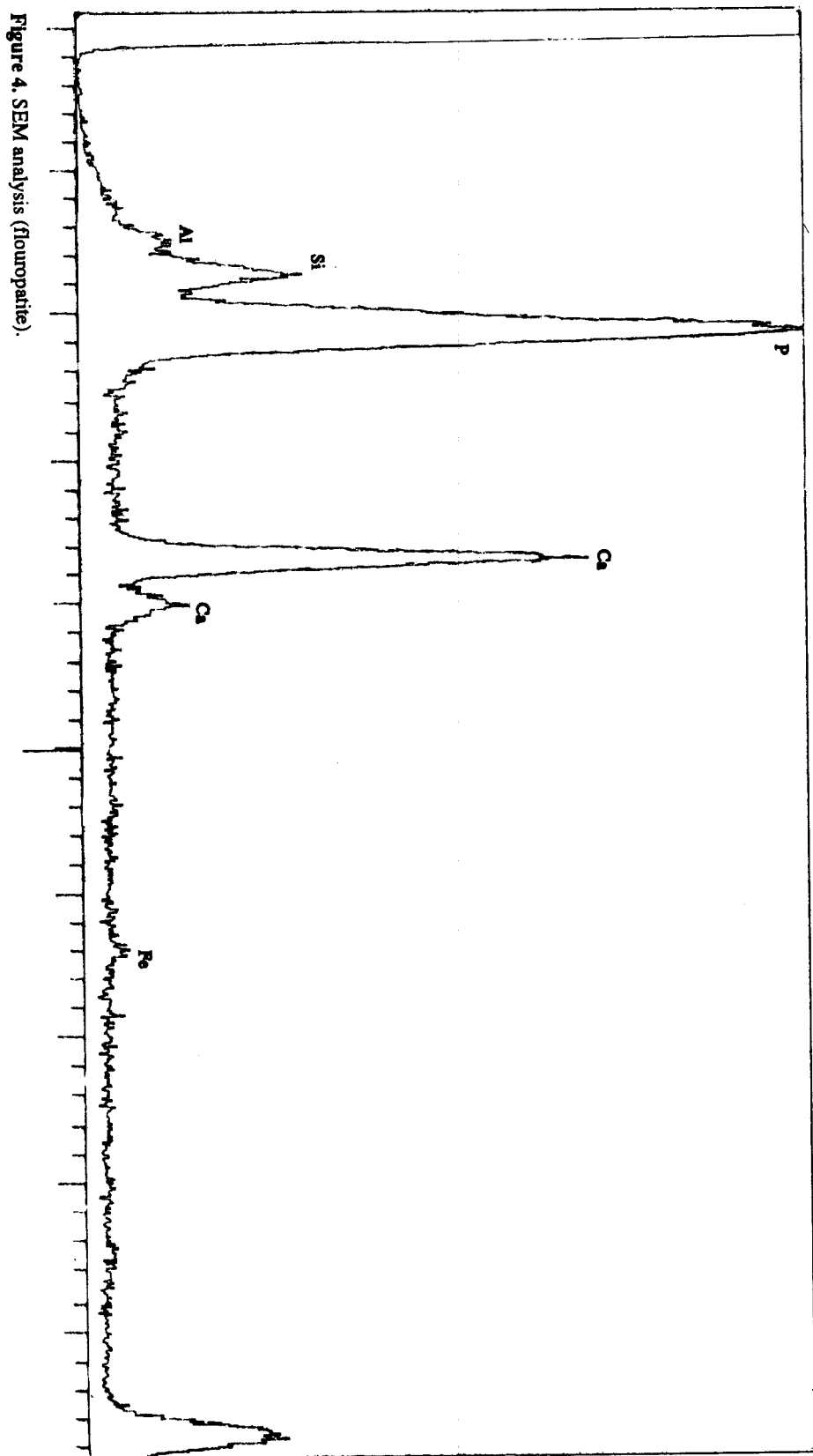


Figure 4. SEM analysis (fluorapatite).

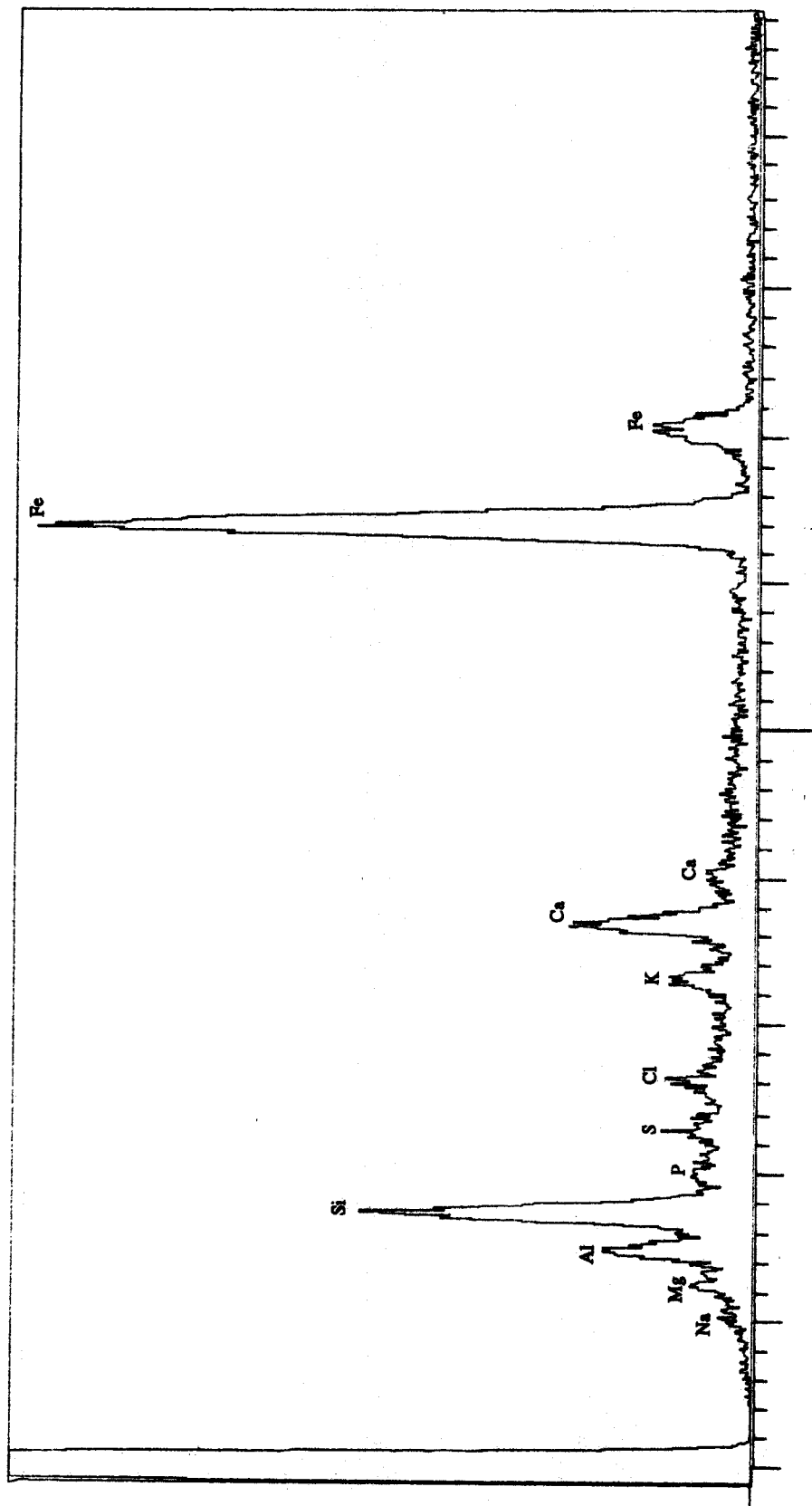


Figure 5. SEM analysis (Pyr: te).

Although the aperture is not completely preserved, there is evidence of partial plate-like extension. Shell moderately thick.

H	W
0.33 mm	0.67 mm

#### Occurrence

This genus occurs in Bed 2 of section A which is referred to as the Upper *gigas* Zone.

Subfamily Bucaniidae ULRICH & SCOFIELD, 1897

Tribe Bucaniides ULRICH & SCOFIELD, 1897

Genus *Bucania* HALL, 1847

Plate 1, Figures 3-5

#### Description

Shell isostrophic, loosely coiled, whorls increase in size moderately and become gradually flattened. Aperture not preserved but from whorl cross-section it is clear that it expanded more in width than in height as much as two times without any sign of a flare. Suture deep, acute, umbilici wide, rather deep, equally concave on both sides, displaying about 1/2 of previous whorls; whorls rising from the suture in an inward curve and then rounding rapidly over the sides to the back which is rather broad, flatly and moderately convex. Shell surface smooth and without any ornamentation.

A	H	W
0.55 mm	1.2 mm	0.95 mm

#### Occurrence

The genus comes from Beds 2 and 6 of section A which are referred to as the Upper *gigas* and uppermost Famennian-Tournaisian. It is also found in Bed 10 of section B with uppermost Famennian to Tournaisian age.

Subfamily Bucaniidae ULRICH & SCOFIELD, 1897

Tribe Bucaniides ULRICH & SCOFIELD, 1897

Genus *Megalomphala* ULRICH & SCOFIELD, 1897

Plate 2, Figure 11

#### Description

Shell isostrophic, widely phaneromphalous, nearly closely coiled. Umbilicus open; from side view with a gentle dorsal carina and probably possessing a selenizone; whorl profile lenticular towards the outer side but on the inner side of the whorl it is arched

towards inner side because of the good development of previous whorl; apertural margins seemingly tending to flare; inner lip well developed; shell nearly thick.

H	W
0.33 mm	0.67 mm

#### Occurrence

*Megalomphala* found in Bed 2 of section A within the range of the Upper *gigas* Zone.

Subfamily Tropidodiscinae KNIGHT, 1956

Genus *Tropidodiscus* MEEK & WORTHEN, 1866

Plate 1, Figures 6-8

#### Description

Shell isostrophic openly coiled with a rather sharp dorsum. Successive whorls, which are less than 2 and 1/2, not in contact but in very constant and close proximity. Whorls tending toward rapid expansion after first whorl. Whorl profile hastate, acutely angulated at the dorsum, gently convex on both sides and sharply rounded on the umbilical side. Umbilici open and largely wide. Shell surface is smooth and without any ornamentation; shell maximum width 1.7 mm.

#### Remarks

In previous explanation of this genus whorls are not disjunct.

#### Occurrence

The genus occurs in Bed 9 and the lower part of Bed 11 of section A which are referred to as the *anchoralis-latus* Zone. It is also found in the lower part of Bed 10 of section B in the uppermost Famennian to Tournaisian range.

Subclass Prosobranchia MILNE EDWARDS, 1848

Order ? Archaeogastropoda THIELE, 1925

Suborder Murchisoniina COX & KNIGHT, 1960

Superfamily Murchisoniacea KOKEN, 1896

Family Murchisoniidae KOKEN, 1896

Genus *Murchisonia* D'ARCHIAC & VERNEUIL, 1841

Plate 2, Figures 7-8

#### Description

Shell almost turritid, anomphalous, with maximum of five whorls seen. Suture grooved, deep and acute. Sinus-band rather wide in the centre of the whorl side,

prominent, concave, bounded by a pair of spiral cords. Whorl profile sloping strongly and flatly outward above the upper of the upper spiral cords, concave between the cords and sloping strongly and flatly inward below the lower cord. A row of tubercles on the shoulder just below the suture is present at least on the last two whorls. Aperture almost quadrangle, base conical; shell moderately thick.

H	W	P	S
0.8 mm	0.56 mm	40°	15°

#### Occurrence

The genus occurs in Bed 2 of section A which is referred to as the Upper *gigas* Zone.

Suborder Mucluritina COX & KNIGHT, 1960  
Superfamily Euomphalacea DE KONINCK, 1881  
Family Euomphalidae DE KONINCK, 1881  
Genus *Phanerotinus* J.D.C. SOWERBY, 1844

Plate 2, Figures 9-10

#### Description

Shell rather discoidal and openly coiled; whorls gradually expanding in size; umbilicus open and largely wide. Shell surface smooth and without any ornamentation. Only 1 1/4 whorls seen; whorl profile circular; shell widths for three specimens are: 0.7 mm, 1.12 mm, and 1.32 mm.

#### Remarks

This genus shows a significant difference from the specimen described in treatise.

#### Occurrence

*Phanerotinus* found in Beds 2 and 11 of section A which are indicated as the Upper *gigas* and *anchoralis-latus* Zones respectively.

Superfamily Euomphalacea DE KONINCK, 1881  
Family Euomphalidae DE KONINCK, 1881  
Genus *Straparollus* DE MONTFORT, 1810

Plate 2, Figures 5-6

#### Description

Shell almost discoidal with wide umbilicus; mostly with three whorls which increase in size very gradually. Whorl profile strongly rounded. Spire slightly elevated in some specimens; in others it is strongly depressed. Inner lip is well developed. Very fine growth line occurs in some specimens. Shell thick

with two distinctly different layers. Shell width 0.6 mm.

#### Occurrence

The genus occurs in Beds 2 and 11 of section A with an age of the Upper *gigas* and *anchoralis-latus* Zones respectively.

Genus *Straparollus* (Philoxen) KAYSER, 1889

Plate 2, Figures 1-4

#### Description

Shell varying from nearly discoidal to depressed spiral; phaneromphalous; with deep narrow to moderately wide umbilicus; spire nearly flat; body whorl tending to make shell form more conical; suture deep and vertical; whorls increasing in size gradually; whorl profile circular; shell surface is not smooth; ornament on the final whorl transverse lira, presumably prosocline; shell moderately thick; shell width 1.5 to 2 times more than height as given below:

W	H
1.5 mm	1.0 mm
2.0 mm	1.0 mm

#### Occurrence

The genus is derived from Bed 2 of section A within the Upper *gigas* Zone.

Superfamily Macluritacea FISHER, 1885  
Family Macluridae FISHER, 1885  
Genus *Maclurites* LESUEUR, 1885

Plate 3, Figures 8-9

#### Description

Shell discoidal with a presumably flattened base and a deeply umbilicate upper surface; whorls increase in size rapidly in first whorl; whorl profile with a rounded angulation and an obscure noth-keel surrounding the umbilicus; the umbilical wall nearly vertical, and the outer wall sloping outward and downward from the noth-keel to the somewhat extended and acutely subangular periphery with gentle convexity; upper umbilical suture sharply incised and moderately deep. Basal suture deep and because it is obscured by the form of attachment, is not exactly clear but according to the unattachment parts, presumably flat or slightly protruding. Shell surface smooth and without ornamentation. Width: 0.73 mm.



**Occurrence**

*Maclurites* comes from Bed 11 of section A which is indicated as the *anchoralis-latus* Zone.

Suborder Pleurotomariina COX & KNIGHT, 1960  
Superfamily Pleurotomariacea SWAINSON, 1840  
Family Raphistomatidae KOKEN, 1896  
Subfamily omospirina WENZ, 1938  
Genus *Callistadia* KNIGHT, 1945

Plate 1, Figure 2

**Description**

Shell relatively low-spired, graded with ramp, narrowly phaneromphalous; short and broad slit, just above nearly vertical outer lip face; whorl profile nearly circular; ornament of spiral cords covering the entire spire; presumably narrow umbilicus; shell rather thick.

H	W	P	S
1.2 mm	1.2 mm	90°	~0°

**Remarks**

The entire surface of the shell has a thin covered layer which obscured the ornaments and even the umbilici; nevertheless the cords and a narrow umbilici are distinguishable.

**Occurrence**

The genus occurs in Bed 6 of section A within the *anchoralis-latus* Zone.

Family Goseleinidae WENZ, 1938  
Subfamily Coelozoninae KNIGHT, 1956  
Genus *Euryzone* KOKEN, 1896

Plate 3, Figures 6-7

**Description**

Shell large, turbiniform with low and depressed spire. Whorl openly coiled and increasing in size gradually; disjunct whorls with very close and constant distance; phaneromphalous; whorl profile well arched between sutures and concave on upper side of whorl which are beneath successive upper whorls. Whorl coiling variable from tight to loose. Whorls differ in number from 2 1/2 to 3 1/2 (mostly tightly coiled). Shell surface smooth and without any ornamentation.

H	W	P
0.63 mm	1.07 mm	~90°

**Occurrence**

*Euryzone* achieved from the lower part of Bed 5 of section A within the Lower *costatus* Zone.

Family Raphischismatidae KNIGHT, 1936  
Genus *Raphischisma* KNIGHT, 1936 (?Rotellina)

Plate 3, Figure 3

**Description**

Shell almost lenticular, low spired. Protoconch is unusually large. Whorls increase in size gradually. Suture deep; phaneromphalous, but mostly covered because of heavy callus or apertural flaring; whorl profile rounded in basal and outer faces when it reaches to high point, especially after first whorl with a distinct angle and concave feature continuing toward the upper whorl.

W	P
0.6 mm	115°

**Remarks**

This specimen differs from *Raphischisma* in having low-conical rather than concave spire. Its chief distinction is the very large protoconch. One of the Whidborne specimens is very similar.

**Occurrence**

The genus occurs in the upper part of Bed 5 of section A referred to as the *costatus* Zone.

Suborder Trochina COX & KNIGHT, 1960  
Superfamily Platyceratacea HALL, 1859  
Family Holopeinae WENZ, 1938  
Subfamily Holopeinae WENZ, 1938  
Genus *Holopea* HALL, 1847

Plate 3, Figure 4

**Description**

Shell turbiniform; moderately elevated spire; whorls about three, increasing in size gradually; whorl profile strongly rounded; suture deep and impressed; nearly anomphalous to minutely phaneromphalous; shell surface smooth and without any ornamentation.

H	W	P	S
1.2 mm	1.2 mm	85°	17°

**Occurrence**

*Holopea* found in the lower part of Bed 11 of section A with *anchoralis-latus* Zone and the lower part of Bed 10 with uppermost Famennian to Tournaisian

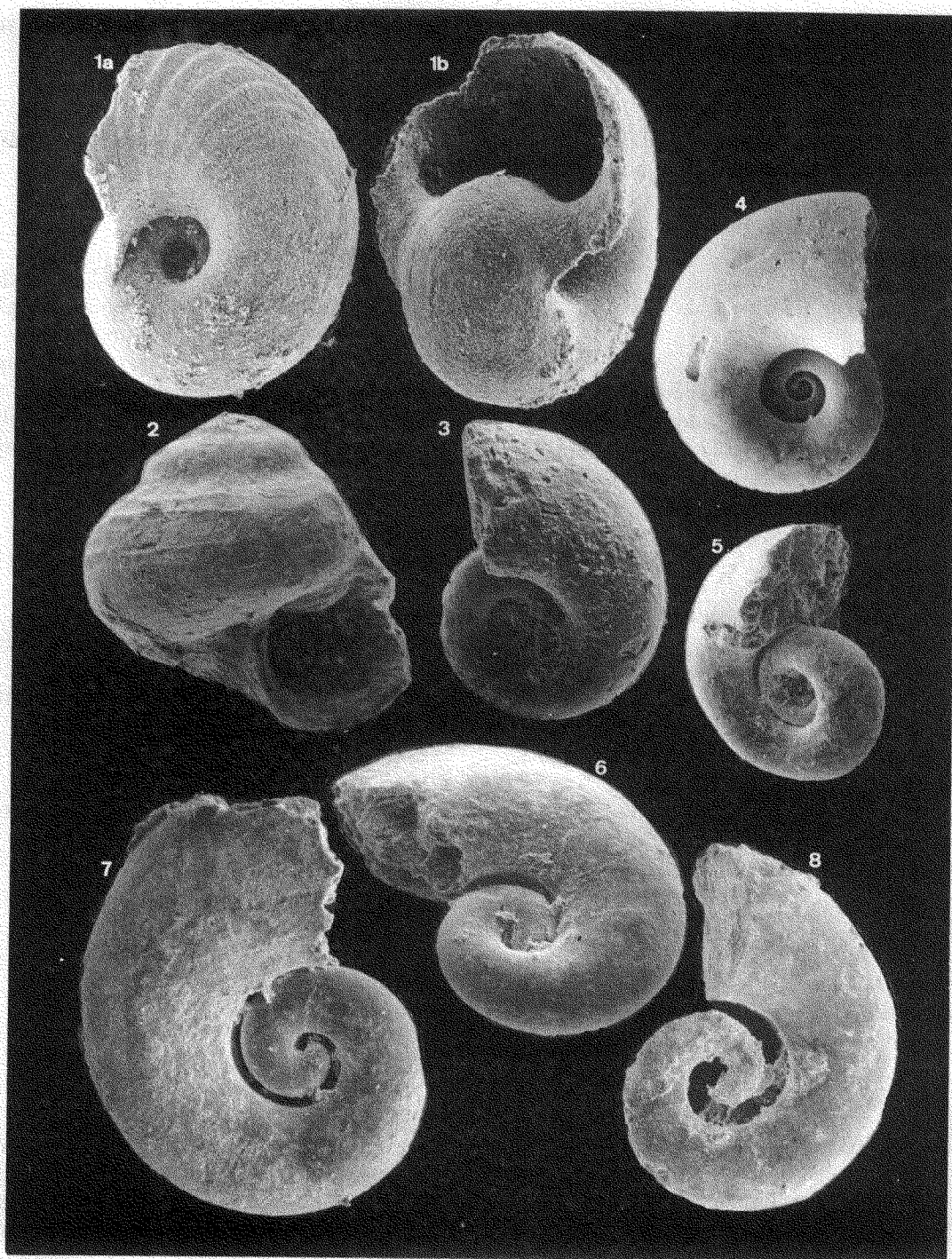


Plate 1

*Bucanopsis*

Figure 1. G.1. (90X)

*Callistadia*

Figure 2. G.5. (180X)

*Bucania*

Figure 3. G.4. (80X)

Figure 4. G.4. (200X)

Figure 5. G.2. (200X)

*Tropidodiscus*

Figure 6. G.2. (90X)

Figure 7. G.2. (80X)

Figure 8. G. 2. (80 X)

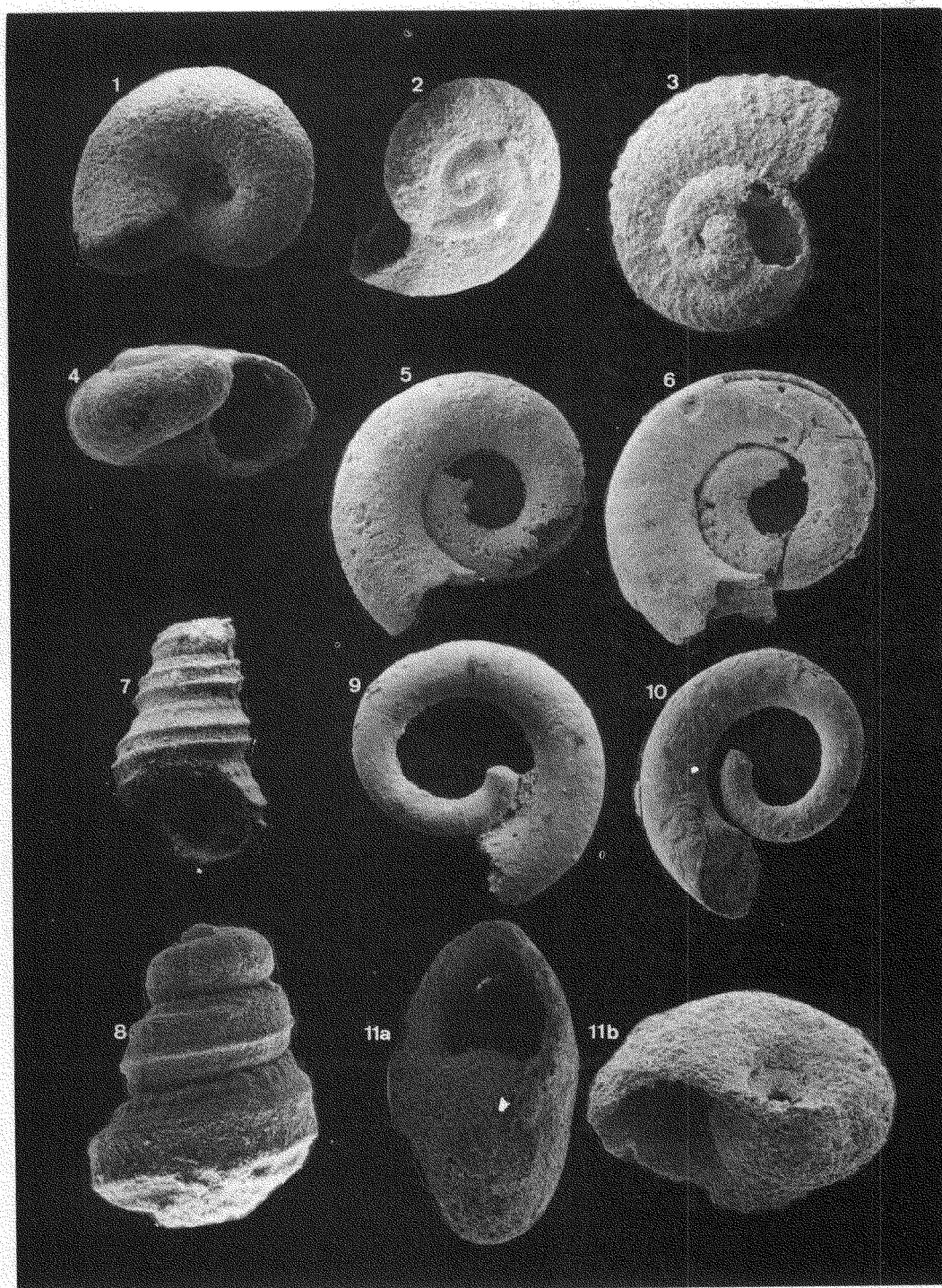


Plate 2

*Straparollus (Philoxen)*

- Figure 1. G.3. (80X)
- Figure 2. G.3. (80X)
- Figure 3. G.3. (80X)
- Figure 4. G.3. (80X)

*Straparollus*

- Figure 5. G.3. (80X)
- Figure 6. G.3. (80X)

*Murchizonia*

- Figure 7. G.1. (100X)
- Figure 8. G.1. (90X)

*Phanerotinus*

- Figure 9. G.7. (200X)
- Figure 10. G.7. (200X)

*Megalomphala*

- Figure 11. G.3. (80X)



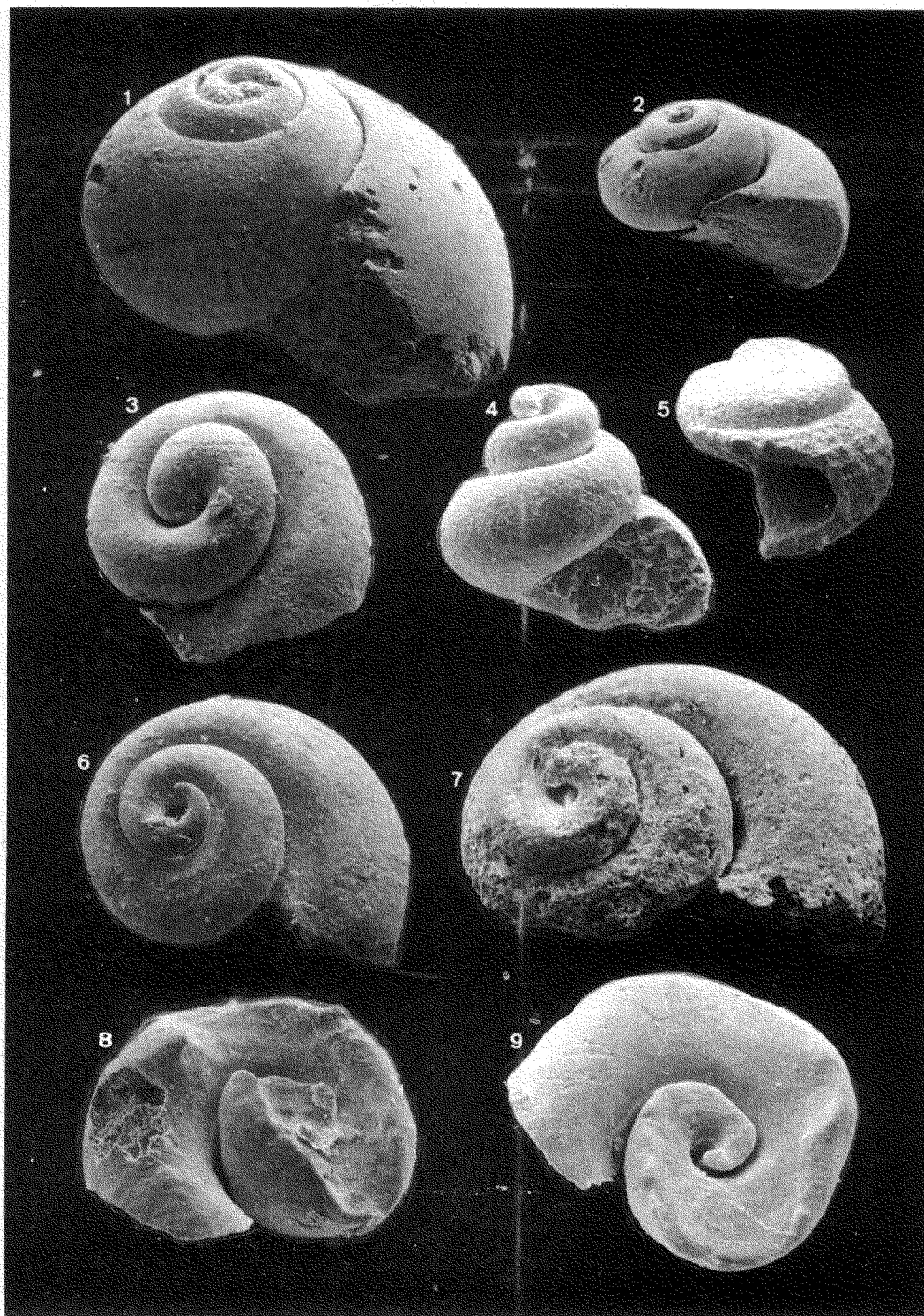


Plate 3

*Naticopsis*

Figure 1. G.1. (90X)

Figure 2. G.5. (180X)

*Raphischisma*

Figure 3. G.5. (90X)

*Holopea*

Figure 4. G.3. (90X)

*Rhabdotocochlis*

Figure 5. G.2. (90X)

*Euryzone*

Figure 6. G.2. (90X)

Figure 7. G.4. (90X)

*Maclurites*

Figure 8. G.7. (90X)

Figure 9. G.7. (90X)

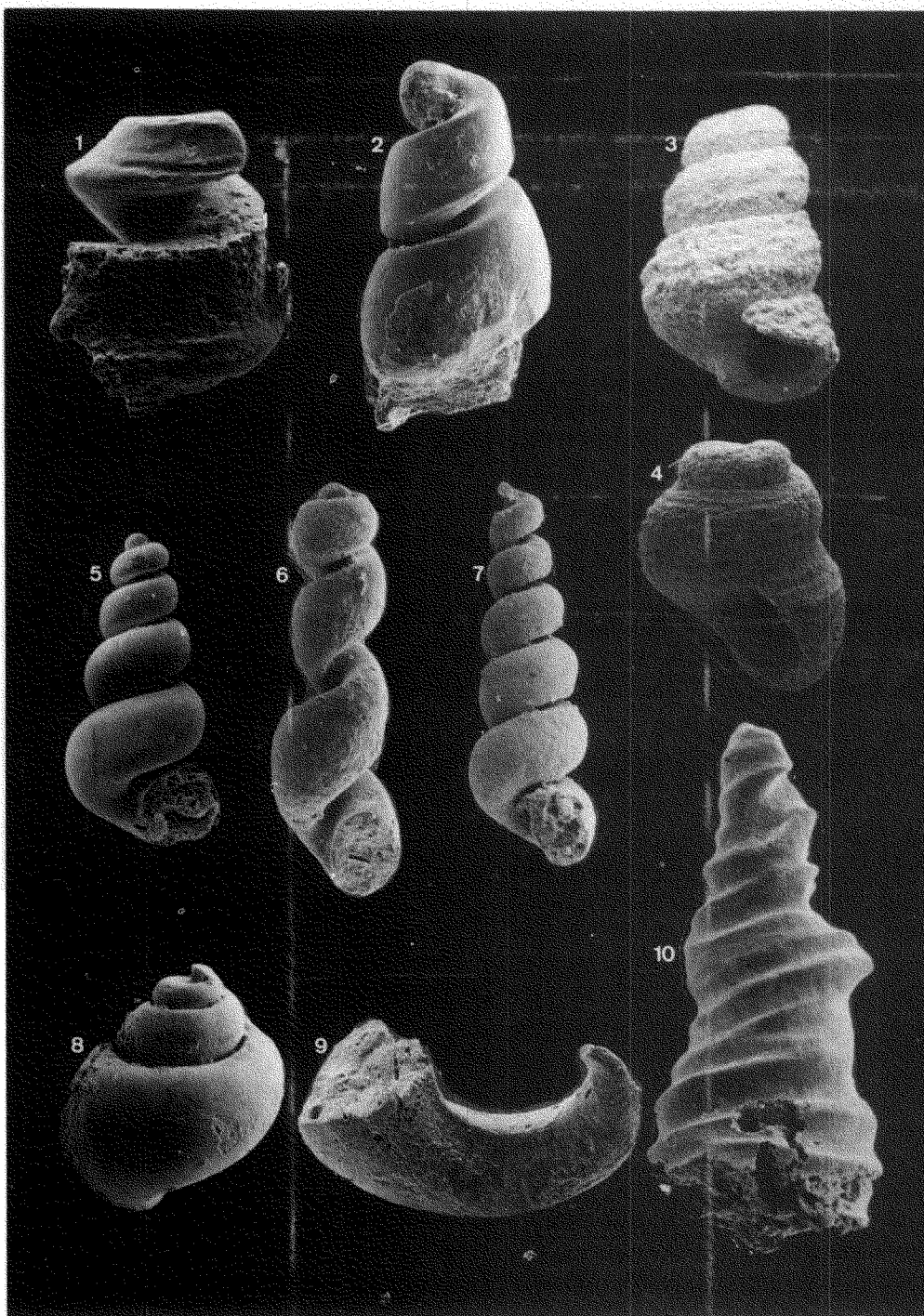


Plate 4

*Plagiothyra*

Figure 1. G.4. (180X)

Figure 2. G.6. (180X)

*Cyclonema*

Figure 3. G.3. (90X)

Figure 4. G.3. (90X)

*Loxonema A*

Figure 5. G.1. (200X)

*Loxonema B*

Figure 6. G.2. (90X)

*Loxonema C*

Figure 7. G.7. (180X)

*Bucanopsira*

Figure 8. G.5. (180X)

*Capulus*

Figure 9. G.6. (200X)

Figure 10. G.6. (180X)

range.

Subfamily Gyronematinae KNIGHT, 1956  
Genus *Rhabdotocochlis* KNIGHT, 1933

Plate 3, Figure 5

#### Description

Shell low-spired turbiniform, minutely phaneromphalous; aperture sub-circular; apertural side nearly flat; suture sharp but shallow; shell thick; whorl profile gently arched between sutures, rounded on the final whorl; ornament firmly constant and characteristic, consisting of numerous fine, regularly spiral cords over the entire surface.

H	W	P	S
0.43 mm	0.45 mm	100°	~0°

#### Occurrence

The genus comes from Bed 2 of section A which is referred to as the Upper *gigas* Zone.

Family Platyceratidae HALL, 1859  
Genus *Cyclonema* HALL, 1852

Plate 4, Figures 3-4

#### Description

Shell turbiniform; anomphalous; spire nearly flat to abapertural; whorl profile typically gently rounded between sutures, in final whorl rounded and subangular where the outer whorl face joins the base. Ornament firmly constant and characteristic, consisting of numerous fine, usually regularly revolving cords over the entire surface.

H	W	P	S
0.55 mm	0.45 mm	85°	45°
0.6 mm	0.40 mm	35°	10°

#### Occurrence

The genus subtracted from Bed 2 of section A which is referred to as the Upper *gigas* Zone.

Suborder Neritopsina COX & KNIGHT, 1960  
Superfamily Neritacea RAFINESQUE, 1815  
Family Neritopsidae GRAY, 1847  
Subfamily Naticopsina S.A. MILLER, 1889  
Genus *Naticopsis* M'COY, 1844

Plate 3, Figures 1-2

#### Description

Shell globular to large globular, neritiform to

naticiform slightly protruding to relatively spiral with two last large whorls and a narrow phaneromphalous with smooth surface and without any ornamentation. Suture impressed, whorls and aperture rising from the suture and expanded rapidly in a direction oblique to axis. Outer lip strongly prosocline.

H	W	P	S
0.7 mm	0.8 mm	100°	8°

#### Occurrence

*Naticopsis* found in Bed 2 of section A which is referred to as the Upper *gigas* Zone.

Family Plagyothyridae KNIGHT, 1956  
Genus *Plagyothyra* WHIDBORNE, 1892

Plate 4, Figures 1-2

#### Description

Shell elevated, trochiform, loosely coiled, the successive whorls not in contact, disjunction constant between all whorls; whorls spreading with a sharp angle both from upper and lower part of outer face obliquely down to adaxial; outer side of the whorls are almost convex, flat or even slightly concave with a sharp acute edge to adaxial; shell surface is smooth and without any ornamentation; aperture height and width are not clear because no complete specimen is available.

H	W	P	S
1.2 mm	0.6 mm	23°	20°
0.6 mm	0.53 mm	47°	20°

#### Remark

Very different from Treatise and Knight specimens, but it conforms with at least one of Whidborne's specimens.

#### Occurrence

The genus occurs in Beds 6 and 11 of section A. They are referred to as the Uppermost Famennian-Tournaisian and *anchoralis-latus* Zone (Upper Tournaisian) respectively.

Subclass Prosobranchia MILNE EDWARDS, 1848  
Order? Archaeogastropoda THIELE, 1925  
Superfamily? Craspedostomatacea WENZ, 1938  
Family Craspedostomatacea WENZ, 1938  
Genus? *Bucanospira* ULRICH IN ULRICH & SCOFIELD, 1897

## Plate 4, Figure 8

**Description**

Shell subturbiniiform, phaneromphalous, nearly loosely coiled; umbilicus narrow; apertural margin tending to flare irregularly, whorl profile subcircular; suture deep; surface smooth without ornamentation.

H	W	P	S
0.8 mm	1 mm	90°	~0°
0.7 mm	0.9 mm	90°	~0°

**Occurrence**

The genus occurs in the lower part of Bed 5 and Bed 6 of section A within the *costatus* and *anchoralis-latus* Zones respectively.

Order Ceanogastropoda COX, 1959  
Superfamily Loxonemataceae KOKEN, 1889  
Family Loxonematidae KOKEN, 1889  
Genus *Loxonema* PHILLIPS, 1841

## Plate 4, Figures 5-7

**Description**

Spiral shell with internal mould shows no contact between successive whorls. With regard to whorl enlargement rate, sutural angle and number of volutions, three different groups are represented.

A. Shell large, with a maximum of five whorls which enlarge very rapidly; with rather large body whorl (Figure 5).

H	W	P	S
0.93 mm	0.60 mm	35°	23°

**Occurrence**

The specimens occur in Bed 2 with an age of the Upper *gigas* Zone (Lower Famennian).

B. Shell slender with whorls enlarging very gradually. Suture in the first two whorls is rather close and not changing rapidly; in the later part of the shell it is much looser and changes rapidly; maximum of four volutions seen (Figure 6).

H	W	P	S
0.87 mm	0.28 mm	25°	20°

**Occurrence**

The specimens occur in the lower part of Bed 11 of section A within the *anchoralis-latus* Zone and Bed 10 of section B with uppermost Famennian age.

C. Shell more elongate up to six whorls which gradu-

ally and very regularly enlarge. Suture regularly changing (Figure 7).

H	W	P	S
1.26 mm	0.4 mm	20°	20°

**Occurrence**

The specimens come from Bed 11 of section A within the *anchoralis-latus* Zone.

?

Family Capulidae, CUVIER  
Genus *Capulus* MONTFORT, 1810

## Plate 4, Figure 9

**Description**

Shell horn-like, enlarges extremely rapidly, planispiral, seen to about one-half of a whorl; outer face convex and rounded, inner surface concave and rounded in one specimen but with a large carina in the other specimen; whorl profile nearly circular, with a ridge formed on inner side of one specimen. Whorl profile increasing in size very rapidly, so that after 1/2 whorl the diameter increases more than 25 times. Surface smooth and without ornamentation.

W	A
1.26 mm	0.46 mm
1 mm	0.86 mm

**Occurrence**

*Capulus* occurs in Bed 11 with an age of *anchoralis-latus* Zone (Upper Tournaisian).

???

## Plate 4, Figure 10

**Description**

Shell conical, straight, without any coiling, highest specimen among all the specimens which have been examined; ornamentation irregular, sharp and coarse coatae, occasionally emerging and disappearing in different parts of the shell; shell attached and the ornamentation obscured; whorl profile nearly circular, increasing in size gradually.

G6 (9)

H	W	C
1.9 mm	0.7 mm	18°

## Occurrence

The genus occurs in Bed 11 which is referred to as *anchoralis-latus* Zone (Upper Tournaisian).

## Conclusion

Microgastropoda fauna from the Upper Devonian and Lower Tournaisian have been examined. In total, 20 genera have been introduced; this is the first description of the early stages of gastropoda.

Almost all specimens are less than 1 mm in size. Generally, they are grey to dark grey in colour. Most specimens show a smooth surface without any ornamentation.

The original aragonite shells of the Upper Devonian species are replaced by pyrite and the Lower Tournaisian species by fluorapatite.

Because of the limited research carried out on the early stage of gastropod, further work on the studied materials could lead to the introduction of new species.

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