Bollettino della Società Paleontologica italiana - Vol. 20, n. 1, 1981, pp. 19-48, pls. 1-6, text-figs. 1-7.

Pygopid brachiopods from the Venetian Alps

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(manuscript received October 16, 1980
accepted January 10, 1981)

KEY WORDS — Brachiopods, Pygopinae, Nomenclature, Systematics, Phylogeny, Upper Jurassic, Lower Cretaceous, Venetian Alps.

ABSTRACT — The Pygopidae contained in the Padua University collection are revised and referred to the species Pygope diphya *(von Buch, 1834),* Pygope catulloi *(Pictet, 1867),* Pygope janitor *(Pictet, 1867),* Pygites diphyoides *(d'Orbigny, 1849),* Triangope triangulus *(Valenciennes, 1819),* Triangope euganeensis *(Pictet, 1867), and* Nucleata planulata *(Zejszner, 1846).*

The new generic name Triangope *is established (type-species* Terebratula triangulus *Valenciennes, 1819). Buckman's theory of the evolution of imperforate from perforate pygopids by loss of the perforation is rejected. Nomenclature of the Pygopinae is discussed and disuse of the generic name* Antinomia *Catullo, 1851 and of some senior synonyms among the specific names is recommended.*

RIASSUNTO — [Brachiopodi pygopidi delle Alpi Venete] — E' stata revisionata la collezione di pygopidi del Museo dell'Istituto di Geologia dell'Università di Padova. Sono state riconosciute le specie Pygope diphya *(von Buch, 1834),* Pygope catulloi *(Pictet, 1867),* Pygope janitor *(Pictet, 1867),* Pygites diphyoides *(d'Orbigny, 1849),* Triangope triangulus *(Valenciennes, 1891),* Triangope euganeensis *(Pictet, 1867) e* Nucleata planulata *(Zejszner, 1846). Viene istituito il nuovo genere* Triangope *con specie-tipo* Terebratula triangulus *Valenciennes, 1819. Viene respinta la teoria di Buckman che fa derivare i pygopidi imperforati da quelli perforati per progressiva chiusura del foro. Viene discussa la nomenclatura delle Pygopinae e si raccomanda l'abbandono del nome generico* Antinomia *Catullo, 1851 nonché l'adozione, per alcune specie, di sinonimi più recenti.*

INTRODUCTION

This paper consists essentially of a revision of the Pygopidae contained in the rich collection in the Museum of the Institute of Geology and Palaeontology of the University of Padua. This material is of particular interest since it contains the type specimens used by T.A. Catullo (1827-1851), the collection of A. De Zigno, which comprehends amongst other specimens most of those used by F.-J. Pictet in establishing *Terebratula euganeensis* (1867), and moreover the pygopine brachiopods collected by G. Dal Piaz (1907) and by many unknown collectors and researchers during a span of time longer than one century.

The specimens studied came from the area comprised between Lake Garda on the west, the Non Valley and the Vette Feltrine on the north, the Piave Valley on the east and the Euganean Hills on the south, and derived from the two classic formations of the Venetian Alps covering the stratigraphical interval from Upper Jurassic to Lower Cretaceous, namely the Rosso Ammonitico Veneto and the Biancone (equivalent of the Lombardian Maiolica) (see text-fig. 1). The material was almost entirely collected by old investigators and the exact position of the specimens in the sequence of the two formations is unknown; because of this, in order to assign them to their correct chronostratigraphical position, we have carried out, when possible, micropalaeontological study of the matrix of the brachiopods and critical analysis of the associated macrofauna quoted in the literature.

The pygopine brachiopods, with their highly distinctive appearance, attracted attention at an early period. Colonna (1606) figured one as *Concha diphya,* which is almost the earliest name to be applied to a brachiopod species and by far the earliest which is still in common use. Colonna's specimen very probably came from the Venetian Alps, the abundant faunas of which have occupied a central position in the study of this group of brachiopods. Catullo (1827) was the first author to deal specifically with this fauna; he was struck by the unusual appearance of the forms which he called *Terebratula antinomia* and was apparently unaware of previously published notices of similar forms elsewhere (« Di tutte le terebratole che ho rinvenute nei monti delle Venete Provincie, quella di cui

mi occupo presentemente è la più grande, ed anche la più singolare per un incavo profondo di figura elittica che si vede nel centro delle due valve, in grazia del quale la conchiglia riesce affatto differente da tutte le altre congeneri »). It was on these same specimens figured by Catullo that Link (1830) founded the genus *Pygope*. The close relationship of the perforate and imperforate pygopines was early recognized, both Parkinson (1811) and Catullo (1827) figuring a mixed collection of perforate and imperforate forms under one specific name.

During the late nineteenth and early twentieth centuries a considerable amount of stratigraphic work was done on the Venetian Alps and Geyssant (1966) gives an extensive bibliography of references to pygopine brachiopods in the area. Ager (1975) remarks that the Pygopidae have been the subject of a great deal of interest and theorizing but remarkably little systematic study; but there has been a revival of interest in them during the last two decades, starting with Jarre's (1962) detailed revision based upon the very representative collection at Grenoble, a work which, astonishingly, makes no reference at all to the internal skeletal structures of the brachiopods. Muir-Wood (1965) established the family Pygopidae and figured some serial sections of *Pygites diphyoides*. Geysssant (1966) made a painstaking review of the geographical and stratigraphical distribution of the main species, with distribution maps. Vogel (1966) analysed the functional morphology of members of the subfamily, concluding that they were adapted for life in an environment of low oxygen pressure. Barczyk (1972) published serial sections of the internal skeletal structures of *Pygope diphya* as did Smirnova (1972) of *Pygope janitor*. Dieni and Middlemiss (1975) established the subfamily Pygopinae. Ager (1975) provided serial sections of *Propygope aspasia, Nucleata rupicola, Antinomia triangulus* and *Pygites diphyoides* which were better than those of earlier authors, as did Middlemiss (1978) of *Pygites diphyoides*.

BUCKMAN'S PHYLOGENETIC THEORY

Buckman's work on the pygopines led him to formulate (1906) a famous theory in which they appeared as an excellent example of the parallel evolution of homochronous homoeomorphs. According to this theory there were three independent lineages, named by Buckman *Antinomia, Pygope* and *Pygites,* each stemming from a different member of the genus *Nucleata* and each passing, during the later Jurassic and early Cretaceous, through a parallel series of morphological changes in which the lateral parts of the shell expanded anteriorly until they met in the centre of the anterior, forming the perforation; following this, evolution continued with the progressive closure of the perforation to give a secondarily imperforate form as the end member of the lineage. For example, the *Antinomia* lineage started, according to Buckman, with *Nucleata planulata* ("glossothyrid stage"), proceeded through a "bifidate stage" (lateral lobes not joined) such as *Antinomia sima* to a "perforate stage" (lobes joined leaving a perforation) such as *Antinomia catulloi* and ended with an "imperforate stage" (without perforation) such as *Antinomia pileus* (= *Pygope triangulus* – see below). A similar evolutionary course was followed by the *Pygope* lineage, ending with *P. euganeensis,* and the *Pygites* lineage, although in this case the imperforate end member was not known.

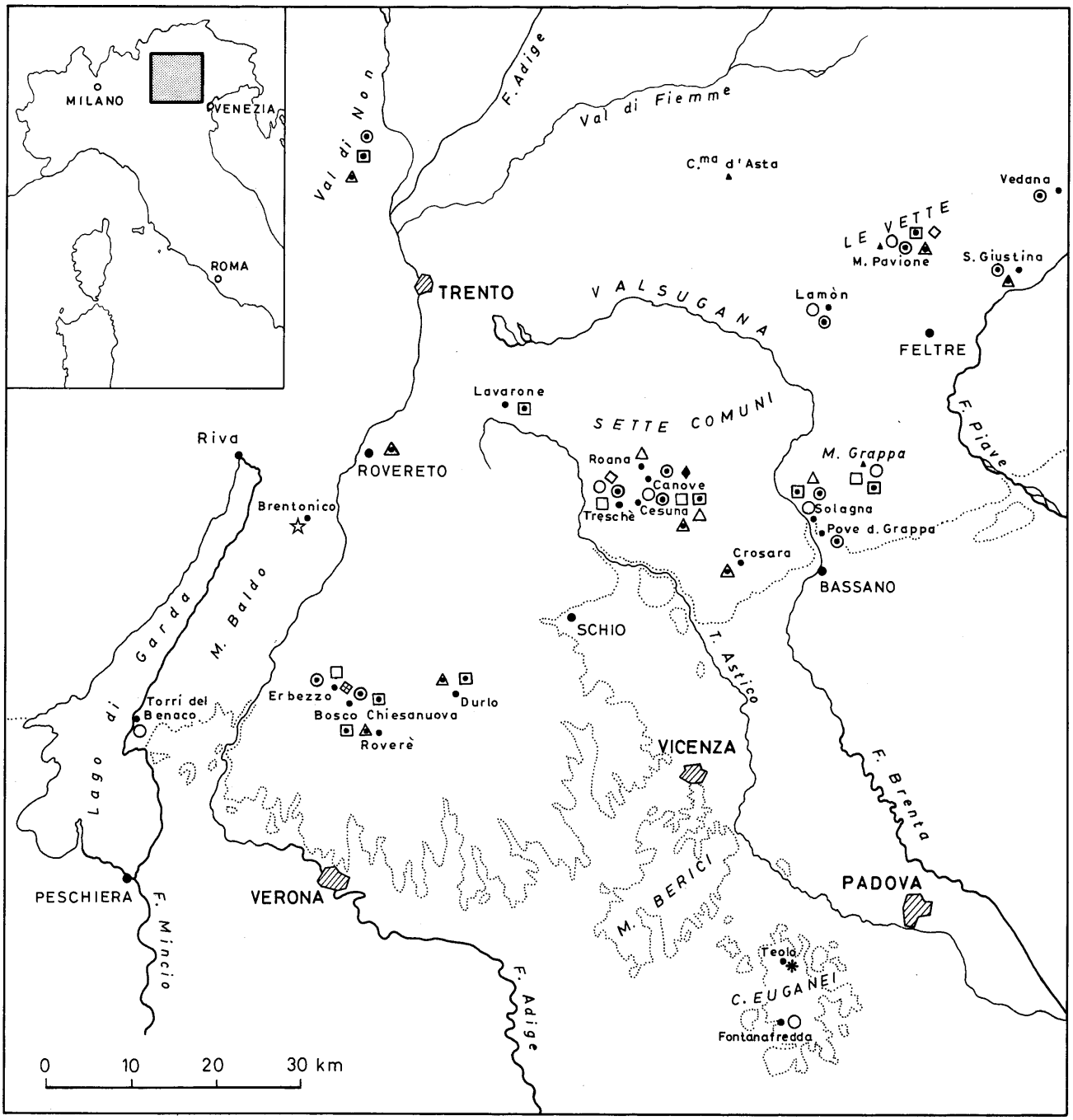
Like Ager (1975) we have been able to examine all the main specimens used by Buckman (British Museum, Natural History), as well as the fine collection at Grenoble used by Jarre and those in other European museums and we agree with Ager in rejecting the most striking part of Buckman's theory. There is no reasonable doubt that the perforate pygopines at least, and probably the imperforate pygopines also, descended from *Nucleata* ancestors and it is probable that different species descended from different species of *Nucleata*; but that imperforate species descended from perforate ones by the closing of the perforation is very unlikely, for the following reasons:

1. There is no stratigraphical evidence for such a succession of forms; the imperforate *Triangope triangulus* is one of the earliest species (text-fig. 2).

2. There is no morphological evidence in the imperforate forms for their derivation from perforate ancestors. One would expect some trace of a scar of the perforation, or at least of a deviation in the growth lines, and also of the sulcus between the conjoined lobes of the shell, but there is none, as Buckman himself remarks.

3. The internal skeletal structures, notably the forms of the hinge plates and crural bases, suggest that the two imperforate species, *T. triangulus* and *T. euganeensis,* are very closely related to each other and less closely related to the perforate species and that they form a separate lineage, perhaps directly descended from a *Nucleata* ancestor.

The lynch-pin of Buckman's theory was the species *Pygope solidescens* Buckman, based on a figure published by Zejszner (1870, pl. 7, figs. 5-7) of a specimen in which the perforation had indeed apparently closed, leaving a distinct scar in the surface of both valves and a narrow sulcus from the scar to the anterior margin. There was only one specimen of this species, that figured by Zejszner, which came from the Tithonian of the Tatra Mountains. We are not aware that any author since Zejszner has seen the specimen which was destroyed in the Second World War (G. Biernat



	R.A.	B.		R.A.	B.
Pygope diphya (v. BUCH)	△	▲	*Pygites diphyoides* (d'ORB.)		♦
Pygope catulloi (PICT.)	□	⊡	*Triangope triangulus* (VALENC.)	○	⊙
Pygope janitor (PICT.)	☆		*Triangope euganeensis* (PICT.)		✱
			Nucleata planulata (ZEJSZN.)	◇	◈

Text-fig. 1 - Locality map of the Venetian Alps between Lake Garda and the Piave Valley (R.A. = Rosso Ammonitico Veneto; B = Biancone).

in litt., September 1979). Zejszner regarded it as a variant of *T. triangulus,* but this is quite incompatible with the complete absence of perforation and sulcus in that species. It may possibly have been a pathological specimen of *P. catulloi* since Zejszner himself compares the shape of the perforation scar to the perforation in that species.

Buckman's terms *glossothyrid, bifidate, perforate* and *imperforate* remain useful in morphological description.

NAMES TO BE APPLIED TO THE PERFORATE AND IMPERFORATE PYGOPINAE

This group of brachiopods has suffered from a plethora of names, many of which can with advantage be discarded.

Generic names

Link (1830) cited as the type material of his new genus *Pygope* the specimens figured by Catullo (1827) as *Terebratula antinomia* (nov.). Catullo's figures are poor and difficult to interpret but one (fig. q) certainly represents the imperforate form *T. triangulus* and the others appear to include the rounded perforate form *Terebratula deltoidea* Valenciennes, 1819 (figs. p and r) (= *Pygope diphya* of this paper) and the triangular perforate form *Antinomia dilatata* Catullo, 1851 (fig. t) (= *Pygope catulloi* of this paper), all of which Link intended to include in *Pygope.* Catullo (1851) founded the genus *Antinomia,* defined by the presence of a deep furrow on the back and of dorsal and ventral perforations, and included six species – *Terebratula diphya* Colonna, *Terebratula deltoidea* Valenciennes, *Terebratulites triquetrus* Parkinson, *Antinomia angulata* nov., *A. angusta* nov. and *A. dilatata* nov. It can therefore be concluded that Link intended *Pygope* to include both perforate and imperforate species and is the valid name, if one should be required, for a genus including both. *Antinomia* was intended by Catullo to apply only to perforate forms but to include both the triangular forms with very small posterior perforation (*A. dilatata, A. angusta* and *A. angulata*) and the rounded forms with somewhat larger and less posterior perforation (*A. deltoidea, A. diphya* and *A. triquetra*).

Catullo (1851) makes no reference to Link's name *Pygope* and was apparently unaware of it; it appears therefore that, as regards perforate forms, *Pygope* and *Antinomia* were synonymous in original intention, both being intended to include all the perforate forms.

It was Buckman (1906) who applied *Antinomia* to both perforate and imperforate forms « in which the perforation (when present) is small and set close to the umbo, while the sides of the valve are flattened, and the side-margin is much curved », and *Pygope* to both perforate and imperforate forms « in which the perforation (when present) is relatively larger and farther removed from the umbo ..... while the sides of the valves are not compressed and the side margin is practically straight ».

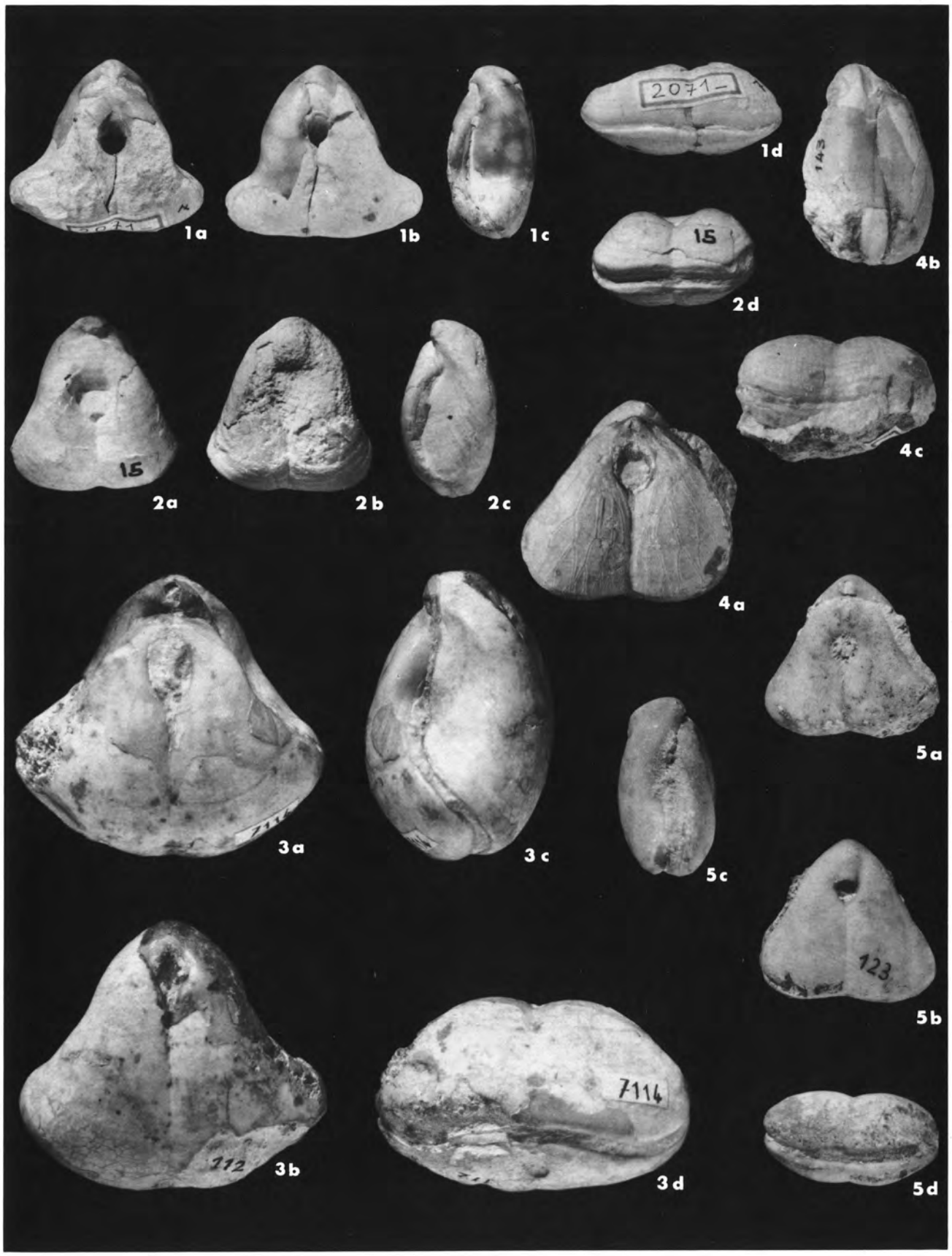
It remains to be discussed whether Buckman's usage of these names serves any useful purpose. Separation of *P. catulloi* (Buckman's *Antinomia*) from. *P. diphya* (Buckman's *Pygope*) is often difficult. Both have a small perforation, more posterior than central; the perforation is oblique, inclined posterior-wards as it passes from dorsal to ventral so that the perforation in the pedicle valve is markedly more posterior than that in the brachial valve. *P. diphya* also has a more rounded shell and *P. catulloi* a more triangular one. In all these characters the differences between the species are only of degree – *P. catulloi* has a still more posterior perforation than *P. diphya* – and the shell shapes are variable. It could be doubted whether the differences are of specific value, let alone of generic value. Geyssant (1966), following Kilian (1910) and Jarre (1962, p. 64), recognized that a transition could sometimes be found between the two species and therefore wished to unite them as *P. diphya* and *P. diphya*

EXPLANATION OF PLATE 1

Figs. 1 - 4 - *Pygope diphya* (Von Buch): 1 a-d) IGP 2071. Upper Tithonian (Biancone), Roveré di Velo. De Zigno Coll. A form with laterally projecting protuberances comparable to Parkinson's *Terebratulites triquetrus.* 2 a-d) IGP 12087. Tithonian (Biancone), Durlo. A form comparable in shape to Valencienne's *Terebratula deltoidea.* Plaster cast of sectioned specimen (see text-fig. 3). 3 a-d) IGP 7114. Biancone, Cesuna. Catullo Coll. A morphotype with concave lateral margins and anterior margin curved backwards. 4 a-c) IGP 18784. Biancone, Sette Comuni. To show the vascular markings of the brachial valve.

Figs. 5 a-d - *Pygope catulloi* (Pictet). IGP 10069 A. Biancone, Cesuna. A morphotype with concave lateral margins.

All figures at natural size.


1a
1b
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1d
143
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15
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15
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3c
5c
123
5b
112
3b
7114
3d
5d

catulloi, with *P. diphya intermedia* to cover the intermediate forms.

It is unfortunate that Buckman (1906, p. 445) failed to recognize the more considerable differences between *P. diphya* and *P. janitor* (Pictet). The specimens used by Buckman (British Museum, Natural History) did not include any clear and unmistakeable examples of the latter species. *P. janitor* has a large central perforation the canal of which is not oblique. We consider therefore that Jarre was correct in recognizing a "small posterior perforation" group (*P. diphya, P. catulloi*) as distinct from a "large central perforation" group (*P. janitor*) and that Ager (1975, p. 156) was wrong to condemn him for this. These two groups could, if one wished, be regarded as subgenera but these would not be Buckman's *Antinomia* and *Pygope* as he included both *diphya* and *janitor* in *Pygope.*

Even the distinction between *P. diphya* and *P. janitor* is not absolutely clear-cut. Several of the topotype specimens of *P. janitor* in the Grenoble collection from La Porte de France, the locality from which the species takes its name, show a perforation nearer posterior than central and slightly oblique. This intermediate type continues as late as the Hauterivian in the Diois.

The conclusion to this discussion is that generic division between *diphya, catulloi* and *janitor* is unnecessary and that Link's name *Pygope* is the appropriate name for them all.

Terebratula diphyoides d'Orbigny is such a distinctive form by reason of the characters of its apical fold and sulcus that a separate generic name is not misleading and is justified. *Pygites* Buckman, 1906 should be applied to this species.

As for the imperforate forms, it has been argued above that these form a separate lineage separable on grounds of both external and internal morphology, as well as of stratigraphic distribution, from the perforate forms. They are therefore here classified in a separate genus, *Triangope* nov. gen.

Specific names

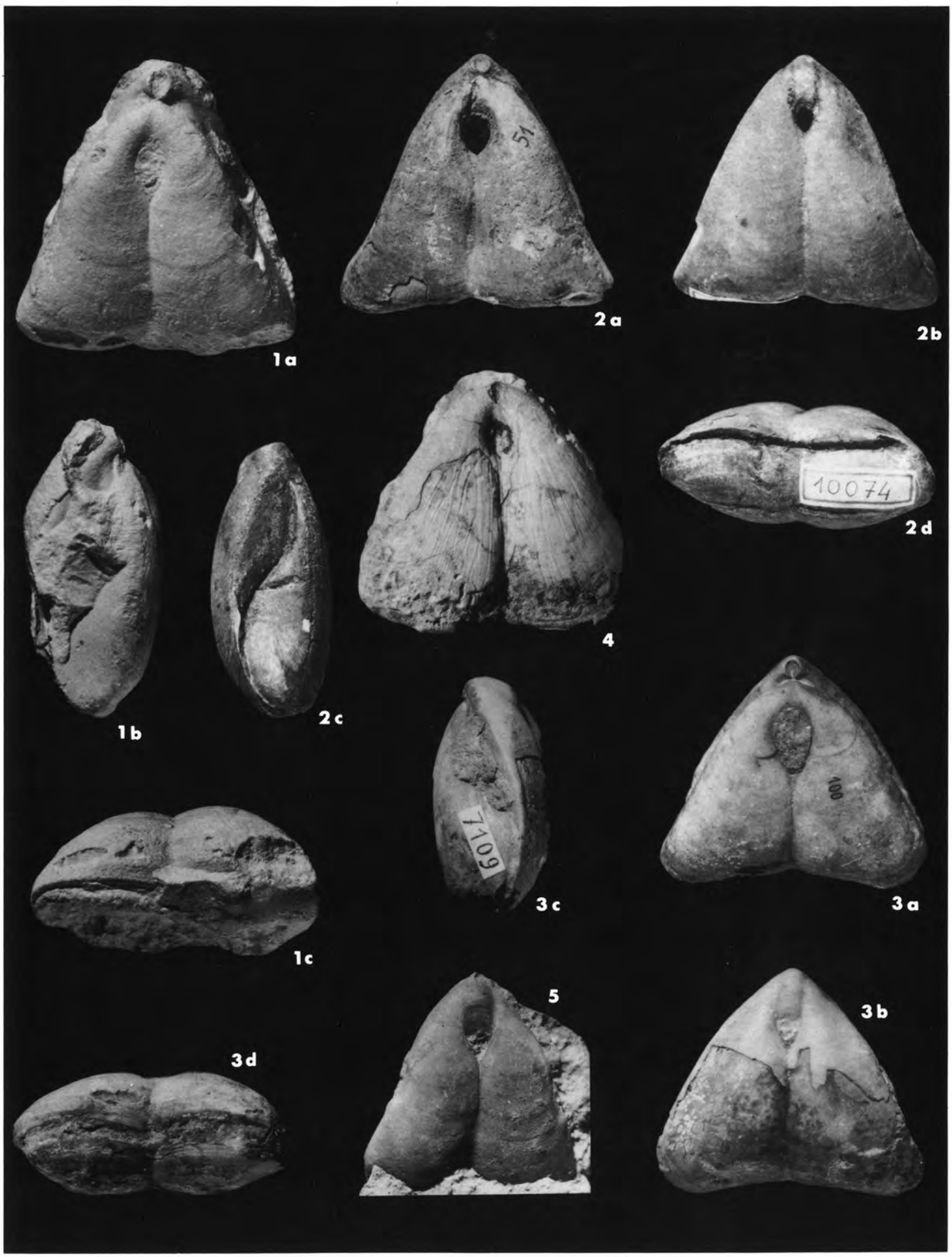
The name *diphya* Colonna, which has been taken by the majority of authors to denote the central specific concept among the pygopines is pre-Linnean. If it is to be used it must be ascribed to the first post-Linnean author to use it, namely von Buch (1834). However, there were several earlier post-Linnean names. Bruguière (1792) named and figured as *Terebratula pileus* and *Terebratula cor* specimens recognizably referable to *T. triangulus* and *P. catulloi* of this paper respectively. Buckman (1906, p. 442) considered that there were significant differences between the mantle canal markings of *T. catulloi* and *T. cor.,* but such differences are not apparent in an examination of his specimens (BM B 8688 and B 16470) (see Plate 3, fig. 3 and Plate 4, fig. 1). In 1797 Bruguière reproduced his 1792 figures, without specific names, together with a third, also unnamed, form recognizable as *P. diphya* of this paper. In 1819 Valenciennes (in Lamarck) gave the name *Terebratula deltoidea* to this third figure but, in ignorance of Bruguière's 1792 paper, gave the name *Terebratula triangulus* to the figure which Bruguière had labeled *T. pileus.* Meanwhile Parkinson (1811) had figured two specimens, one imperforate and undoubtedly conspecific with *T. pileus* Bruguière, the other perforate and probably to be referred to *P. diphya* of this paper; both of these he called *Terebratulites triquetrus.*

Catullo (1827), as stated above, figured a mixture of perforate and imperforate forms as *Terebratula antinomia.* Later (Catullo 1829) he figured as *Terebratula mutica* a typical *T. triangulus* and as *Terebratula antinomia* a form probably to be identified with *P. catulloi.* Later still (Catullo 1841) he reprinted the 1829 *T. antinomia* and *T. mutica* and also reproduced as *Terebratula deltoidea* Bruguière's figure to which Valenciennes had given that name. Finally Catullo (1851) introduced the six specific names *Antinomia diphya, A. deltoidea, A. triquetra, A. angulata, A. angusta* and *A.*

EXPLANATION OF PLATE 2

Figs. 1 - 5 - *Pygope catulloi* (Pictet): 1 a-c) IGP 738. Tithonian (Rosso Ammonitico), Tresché. De Zigno Coll. Plaster cast of sectioned specimen (see text-fig. 4). 2 a-d) IGP 10074. Tithonian (Rosso Ammonitico), Tresché. Triangular form. 3 a-d) IGP 7109. Paralectotype. Rosso Ammonitico, Cesuna. Catullo Coll. (Syntype of *Antinomia angulata* Catullo, 1851). 4) IGP 756. Upper Tithonian (Biancone), Sette Comuni. De Zigno Coll. A form comparable to Bruguière's *Terebratula cor,* showing the vascular markings in the brachial valve. 5) IGP 7106. Biancone, Cesuna. Catullo Coll. Holotype of *Antinomia angusta* Catullo, 1851.

All figures at natural size.


1a
2a
2b
1b
2c
4
2d
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1c
7109
3c
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3b

dilatata, illustrating *A. diphya* by a reproduction of Colonna's figure and *A. deltoidea* by a reproduction of Bruguière's figure. For *A. angulata, A. angusta* and *A. dilatata* he provided sketch figures difficult to link with certainty to actual specimens (the probable type specimens are in the Padua collection, see p. 29), while *A. triquetra* he left unillustrated. Subsequent authors have reasonably taken *A. dilatata* to be the same species as that represented by his 1829 figure of *Terebratula antinomia.* Pictet (1867) redescribed *dilatata,* using Catullo's specific name but decided against adopting his generic name, and called it *Terebratula dilatata.* Later (still in 1867) Pictet realised that he had created a secondary homonym of *Terebratula dilatata* Lamarck and *Terebratula dilatata* Sowerby, so he changed the name of the species to *Terebratula Catulloi.* Although this change of name now seems unnecessary, the name *catulloi* must, under Article 59 (b) (i) of the International Rules, be accepted as the valid name of the species, since the replacement name of the secondary homonym was published before 1961.

To summarize: *Terebratula pileus* Bruguière, 1792, is a senior objective synonym of *Terebratula triangulus* Valenciennes, 1819. *Terebratula* cor Bruguière, 1792 is a senior subjective synonym of *Antinomia dilatata* Catullo, 1851 (and hence of *Terebratula dilatata* Pictet, 1867 and *Terebratula Catulloi* Pictet, 1867). *Terebratulites triquetrus* Parkinson, 1811 is a senior subjective synonym of *Terebratula triangulus* Valenciennes, 1819 and of *Terebratula diphya* von Buch, 1834. *Terebratula deltoidea* Valenciennes, 1819 is a senior objective synonym of *Terebratula diphya* von Buch, 1834 (since von Buch in 1834 cited *T. deltoidea* Lamarck in synonymy and in his 1838 paper reproduced as *T. diphya* Bruguière's 1797 figure upon which Valenciennes had based *deltoidea*). *Terebratula antinomia* Catullo, 1827 is a senior subjective synonym of *Terebratula diphya* von Buch, 1834 and *Antinomia dilatata* Catullo, 1851 (and hence of *Terebratula dilatata* Pictet, 1867 and *Terebratula Catulloi* Pictet, 1867).

Nevertheless, the great majority of authors have used the names *triangulus, diphya* and *catulloi* for the three species groups concerned. *Terebratula pileus* Bruguière, *Terebratula cor* Bruguière, *Terebratulites triquetrus* Parkinson and *Terebratula antinomia* Catullo can all justifiably be considered as forgotten names. This could also apply to *Terebratula deltoidea* Valenciennes but for the action of Muir-Wood (1965) in using this name in the Treatise (part H) with the clear intention of establishing it as the valid name of the species. A further complication here is that the specimen figured by Muir-Wood is not, in fact, a *Pygope deltoidea* (= *diphya*) but a *Pygope janitor.*

Since the name *diphya* (a) is of great historic interest as being by far the oldest brachiopod specific name still in common use and (b) has been used by the great majority of authors as if it were the valid name of the species, it seems desirable in the interests of nomenclatural stability to conserve the name. For the second of these reasons it is desirable to conserve the names *triangulus* and *catulloi. Pygope janitor* (Pictet, 1867) also has a subjective senior synonym in *Terebratula Duvalii* Newman, 1844, which is certainly a forgotten name.

Application is therefore being made to the International Commission on Zoological Nomenclature (Middlemis 1982) to use its plenary powers to suppress the names *Terebratula pileus* Bruguière, 1792, and *Terebratula deltoidea* Valenciennes, 1819; and also to give nomenclatural precedence to *Terebratula triangulus* Valenciennes, 1819, over *Terebratulites triquetrus* Parkinson, 1811; *Terebratula diphya* von Buch, 1834, over *Terebratulites triquetrus* Parkinson, 1811, and *Terebratula antinomia* Catullo, 1827; *Terebratula Catulloi* Pictet, 1867, over *Terebratula cor* Bruguière, 1792, *Terebratula antinomia* Catullo, 1827, and *Terebratula antinomia* Catullo, 1829, 1841; and *Terebratula janitor* Pictet, 1867 over *Terebratula Duvalii* Newman, 1844.

Fortunately *Pygites diphyoides* (d'Orbigny, 1849) and *Terebratula euganeensis* Pictet, 1867, pose no nomenclatural problems.

STRATIGRAPHIC DISTRIBUTION OF THE PERFORATE AND IMPERFORATE PYGOPINAE

These genera present a splendid example of an evolutionary burst, consisting of the abrupt develop-

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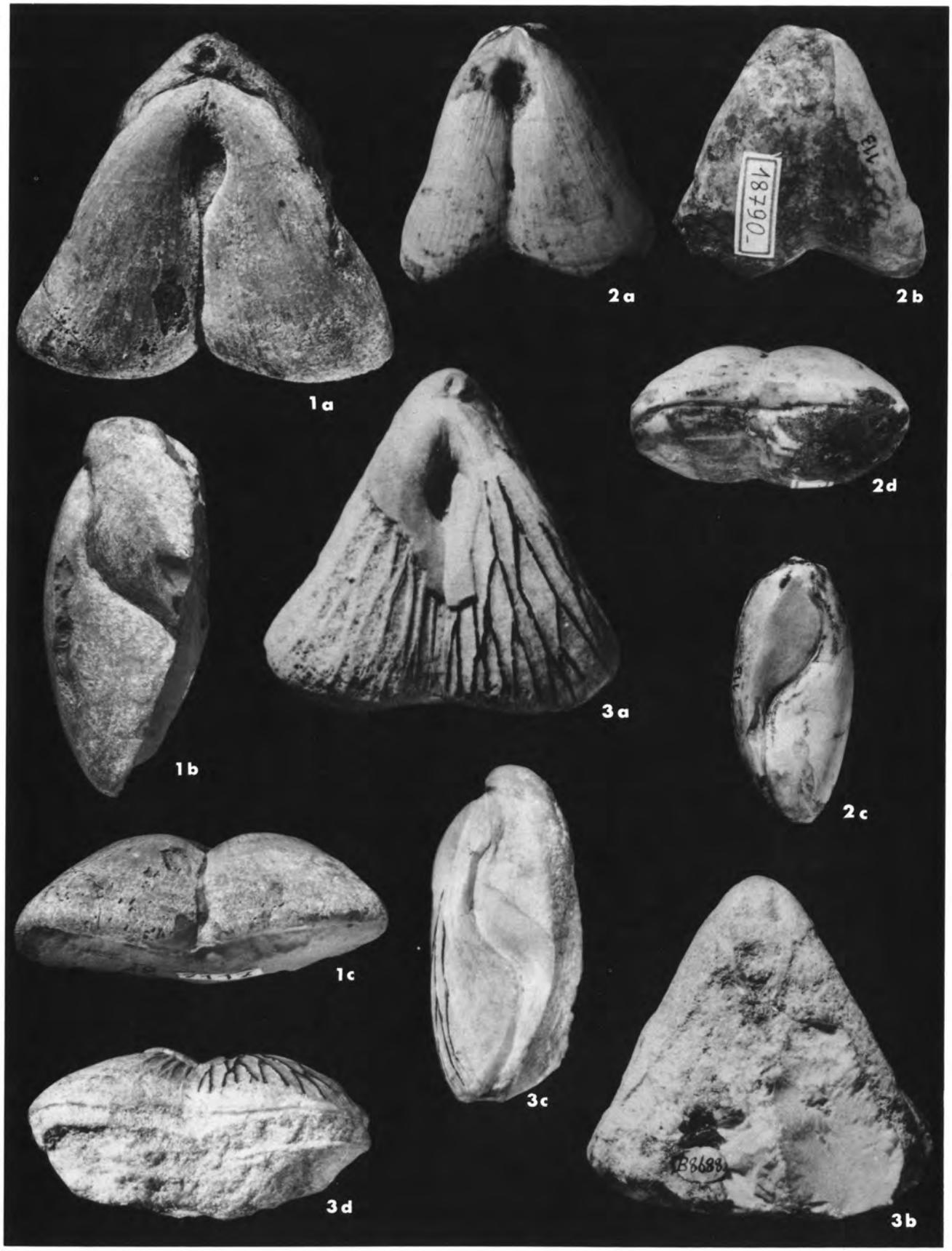
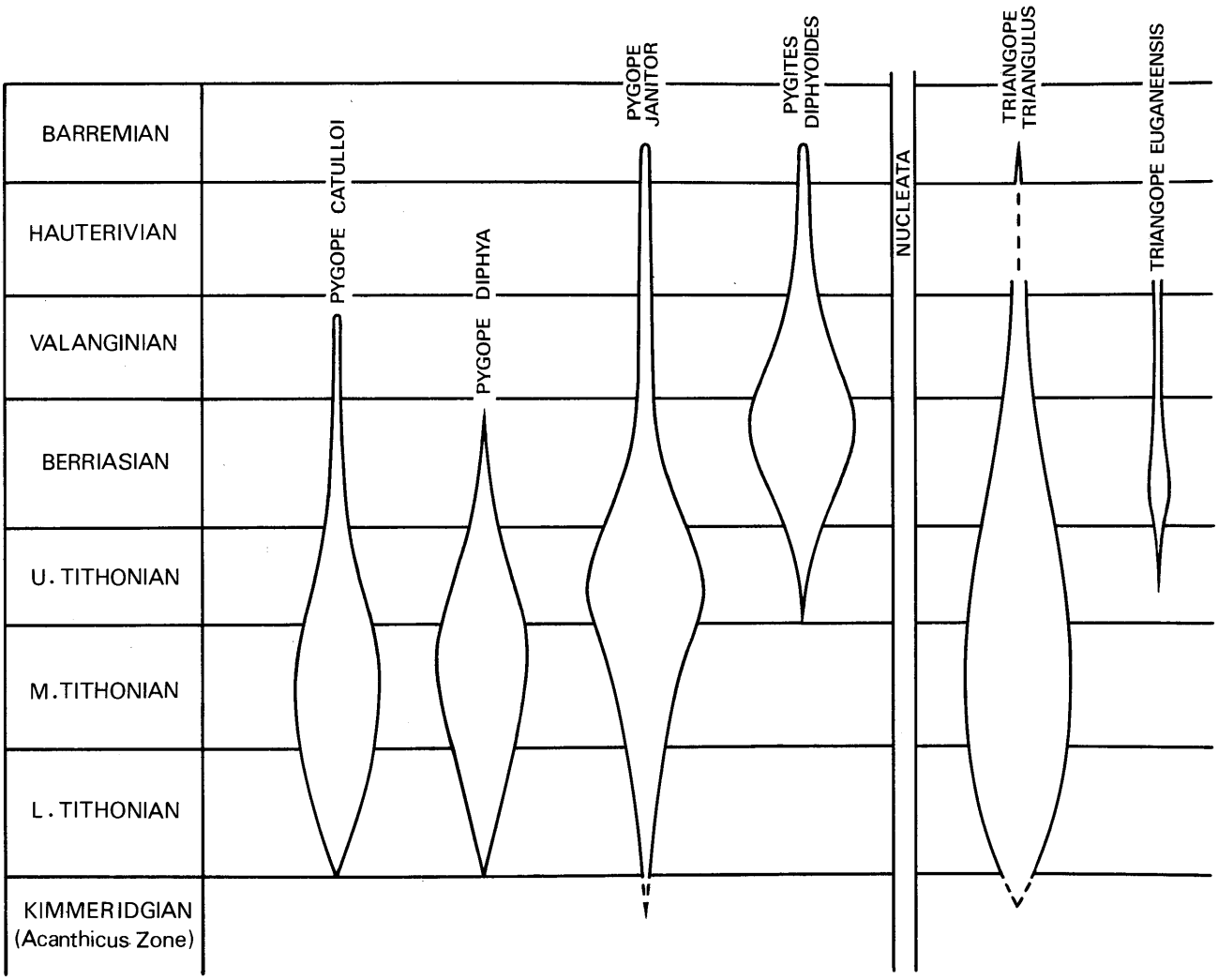
EXPLANATION OF PLATE 3

Figs. 1-3 - *Pygope catulloi* (Pictet): 1 a-c) IGP 7117. Lectotype. Rosso Ammonitico, Cesuna. Catullo Coll. (Syntype of *Antinomia dilatata* Catullo, 1851). 2 a-d) IGP 18790. Biancone, Sette Comuni. Triangular morphotype, showing the vascular markings in the brachial valve. 3 a-d) BM B 8688. « Diphya-Kalk », Trento. Specimen referred to by Buckman 1906, p. 442, as showing the vascular markings well.

All figures at natural size.


1a
2a
2b
18790
113
2d
1b
3a
2c
1c
3c
3d
B3688
3b

ment, from a long-lived conservative stock, of a whole group of strikingly adapted forms which flourished during a clearly defined span of geological time. The *Nucleata* group lived successfully, with only the most minor changes of shape, from the Early Jurassic or earlier into the later Albian, confined to the Tethyan fauna but within that fauna tending to occur in relatively shallow-water sediments, including neritic bioclastic limestones (e.g. northern and eastern Spain). With the Middle Kimmeridgian and Tithonian there developed in the Tethyan region the familiar very fine-grained, deeper-water, light-grey, white or pink limestones of those stages and, in a remarkably short period of time, certain *Nucleata* groups became adapted to the newly available environment. They greatly expanded the lateral and anterior margins of the shell in order to be able to exploit low-energy and low-oxygen conditions (Vogel 1966), some expanding the anterior margin continuously (*Triangope*) and others expanding two lateral lobes until they met in the centre (*Pygope*).



Text-fig. 2 - Stratigraphical distribution of the principal species of the Pygopinae which occur in the Venetian Alps.

These ideal conditions were rare in the Cretaceous and so these genera, and more particularly *Pygites*, adapted themselves to shallower and less purely calcareous conditions such as those found in the Berriasian of Berrias and in the Fosse Vocontienne. Continuing change of conditions, however, caused these genera to be less successful after the Berriasian and the last had become extinct by the middle of the Barremian. The Bakony Forest region seems to have been their last refuge (Fülop 1964).

Text-fig. 2 attempts to bring up to date the similar diagram given by Jarre (1962, fig. 7).

In the present state of knowledge, the early Jurassic imperforate, axiniform, *triangulus*-like species « *Terebratula* » *erbaensis* Suess, « *Terebratula* » *helenae* Renz and « *Terebratula* » *adnethensis* Suess are here regarded as a separate evolutionary radiation.

CATULLO'S TYPE SPECIMENS

Catullo's figures are invariably poor and difficult to interpret. In particular, his illustrations to his 1851 paper are sketches, apparently intended to be generalized rather than to represent individual specimens. However, all the Catullo Collection is in the Institute of Geology and Palaeontology at Padua and certain specimens there have been kept apart as those upon which he based his species. These are:

These are:

IGP 7106A, Tithonian (Biancone), Durlo, and IGP 7117, Tithonian (Rosso Ammonitico), Cesuna: syntypes of *Antinomia dilatata* Catullo, 1851.

IGP 7106, Tithonian (Biancone), Cesuna: type of *Antinomia angusta* Catullo, 1851.

IGP 7108, Tithonian (Rosso Ammonitico), Cesuna, and IGP 7109, Tithonian (Rosso Ammonitico), Cesuna: syntypes of *Antinomia angulata* Catullo, 1851.

IGP 7111, Rosso Ammonitico, Cesuna: type of *Antinomia deltoidea* Catullo 1851.

The originals of the figures given in his earlier papers are almost impossible to trace but there is a specimen in the collection which agrees well with his 1827 pl. 5 fig. r (*Terebratula antinomia*); this is IGP 12029, « Upper Tithonian » (Biancone), Rovereto.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Class ARTICULATA Huxley, 1869
Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily TEREBRATULACEA Gray, 1840
Family PYGOPIDAE Muir-Wood, 1965
(emend. Dieni & Middlemiss 1975)

Diagnosis — Terebratulacea lacking true attached crural bases. The hinge plates are horizontal, tapering or with rounded inner edges, and pass forwards as horizontal structures to join the crura. The loop is short and the transverse band low-arched.

Subfamily PYGOPINAE Dieni & Middlemiss, 1975

Emended diagnosis — Pygopidae with deeply sulcate or triangular shell; the shell may develop two lateral lobes which may curve towards each other and fuse in the adult stage, enclosing a median perforation.

Genus PYGOPE Link, 1830

Type species (by subsequent designation of Buckman 1906, p. 445) — *Terebratula antinomia* Catullo, 1827, fig. r (= *Terebratula deltoidea* Valenciennes, 1819 = *Terebratula diphya* von Buch, 1834).

Synonym — 1851 *Antinomia* Catullo *pro parte.*

Emended diagnosis — Pygopinae with erect to incurved umbo; foramen oval, permesothyrid; deltidium extremely small or invisible; beak ridges round. Shell deeply sulcate in juvenile (glossothyrid) stage, becoming bifidate, and perforate in adult. Apical ventral fold and apical dorsal sulcus present in adult. Perforation central or posterior of centre; perforation canal straight or oblique. Hinge plates horizontal to slightly convex, narrow with blunt inner margins; free crural bases given off ventrally from the anterior ends of the hinge plates, more or less rectangular in section; hinge sockets deep.

Species included — *Terebratula diphya* von Buch, 1834, *Terebratula Catulloi* Pictet, 1867, *Terebratula janitor* Pictet, 1867, *Terebratula sima* Zejszner, 1846, *Terebratula discissa* Zittel, 1870.

Range of the genus — Upper Kimmeridgian to Barremian.

PYGOPE DIPHYA (von Buch, 1834)
Pl. 1, figs. 1-4. Text-fig. 3.

?	1606	*Concha diphya* - COLONNA, p. XXXVI, p. L of section « *Aquatilium et Terrestrium...* ».
	[1797]	*Terebratula* - [BRUGUIÈRE], pl. 240, figs. 4 a,b.
pars	1811	*Terebratulites triquetrus* - PARKINSON, p. 229, pl. 16, fig. 4 (*non* fig. 8).
v	1819	*Terebratula deltoidea* - VALENCIENNES *in* LAMARCK, p. 250, no. 20.
v pars	1827	*Terebratula antinomia* - CATULLO, p. 169, pl. 5, figs. p, r (*non* figs. q, t; ?s).
+	1834	*Terebratula diphya* Colonna - VON BUCH, p. 88, pl. 1, fig. 12.
	1838	*Terebratula diphya* Colonna - VON BUCH, p. 196, pl. 18, fig. 9.
	1838	*Terebratula diphya* Colonna - BRONN, p. 652, pl. 30, fig. 14.
?	1841	*Terebratula diphya* Colonna - CATULLO, pl. 2, fig. 1.
	1841	*Terebratula deltoidea* Lamarck - CATULLO, p. 238, pl. 2, fig. 3.
pars ?	1846	*Terebratula diphya* Colonna - ZEJSZNER, p. 15, pl. 1, figs. 1, 2-8. (?*non* fig. 2).
v	1850	*Terebratula deltoidea* Valenciennes - DAVIDSON, p. 437, pl. 13, fig. 20.
?	1851	*Antinomia diphya* Colonna - CATULLO, p. 75, fig. 3.

v 1851 *Antinomia deltoidea* Lamarck - CATULLO, p. 75, fig. 3.
1867 *Terebratula diphya* von Buch - PICTET, p. 166, pl. 31, figs. 1-9.
1870 *Terebratula diphya* Colonna - ZITTEL, p. 126, pl. 13, figs. 1-10.
1871 *Terebratula diphya* von Buch - QUENSTEDT, p. 362, pl. 47, fig. 123.
1871 *Terebratula diphyoides* d'Orbigny - QUENSTEDT, p. 365, pl. 48, figs. 1,2.
v 1906 *Pygope deltoidea* (Valenciennes) - BUCKMAN, p. 445, pl. 41, fig. 13
v 1906 *Antinomia triquetra* (Parkinson) - BUCKMAN, p. 443, pl. 41, fig. 9.
v pars 1907 *Terebratula (Pygope) diphya* Col. - DAL PIAZ, p. 150, 152.
v 1910 *Terebratula deltoidea* Valenciennes in Lamarck - CLERC & FAVRE, pl. 4, figs. 21 a-d.
v 1962 *Pygope diphya* (Colonna) - JARRE, p. 48, fig. 5, pl. D, figs. 1-3; pl. E, figs. 1a,b.
1964 *Pygope diphya* (von Buch) - HÖLDER, p. 166-167, text-fig. 47 (6,7).
non 1965 *Pygope deltoidea* (Valenciennes) - MUIR-WOOD, fig. 678 (1a-c).
1966 *Pygope diphya* - VOGEL, pl. 39, fig. 7.
1966 *Pygope diphya* (von Buch) - GEYSSANT, p. 78, pl. 3, fig. 2.
v non 1972 *Pygope diphya* (Colonna) - BARCZYK, pl. 4, figs. 1,2.
v 1972 *Pygope diphya* (Colonna) - BARCZYK, pl. 1, fig. 2.
non 1976 *Pygope diphya* - AVRAM, p. 59, pl. 10, fig. 15.
? 1979 *Pygope diphya* (Columna) - SIBLIK, p. 54, pl. 5, fig. 3.

Holotype — Lamarck's specimen of *Terebratula deltoidea*, fig. Clerc & Favre 1910, pl. 4, figs. 21a-d. The specimen is in the Muséum d'Histoire Naturelle at Geneva. Buckman (1906, p. 447) chose Pictet's (1867) pl. 31, fig. 1 as lectotype of *P. diphya*. However, as it has been shown (p. 26) that *P. dipha* (von Buch) and *P. deltoidea* (Valenciennes) are objective synonyms, the type must be that of the earlier species.

Dimensions of holotype — L = 43 mm, W = 51 mm; thickness not measurable.

Material — 32 specimens from the Rosso Ammonitico and the Biancone of the Venetian Alps (text-fig. 1).

Diagnosis — *Pygope* sub-triangular in ventral profile, the anterior lateral angles rounded; anterior margin indented or not indented. Dorsal perforation oval, posterior of centre; perforation tube obliquely curved so that the perforation in the pedicle valve is more posteriorly situated than that in the brachial valve; ventral perforation small, rounded triangular in shape. Ventral apical fold boldly arched and bordered laterally by narrow and shallow depressions. Dorsal apical sulcus smooth, not clearly marked off from the general curve of the valve. Anterior commissure rectimarginate to uniplicate. Anterior view about equally divided between pedicle and brachial valves.

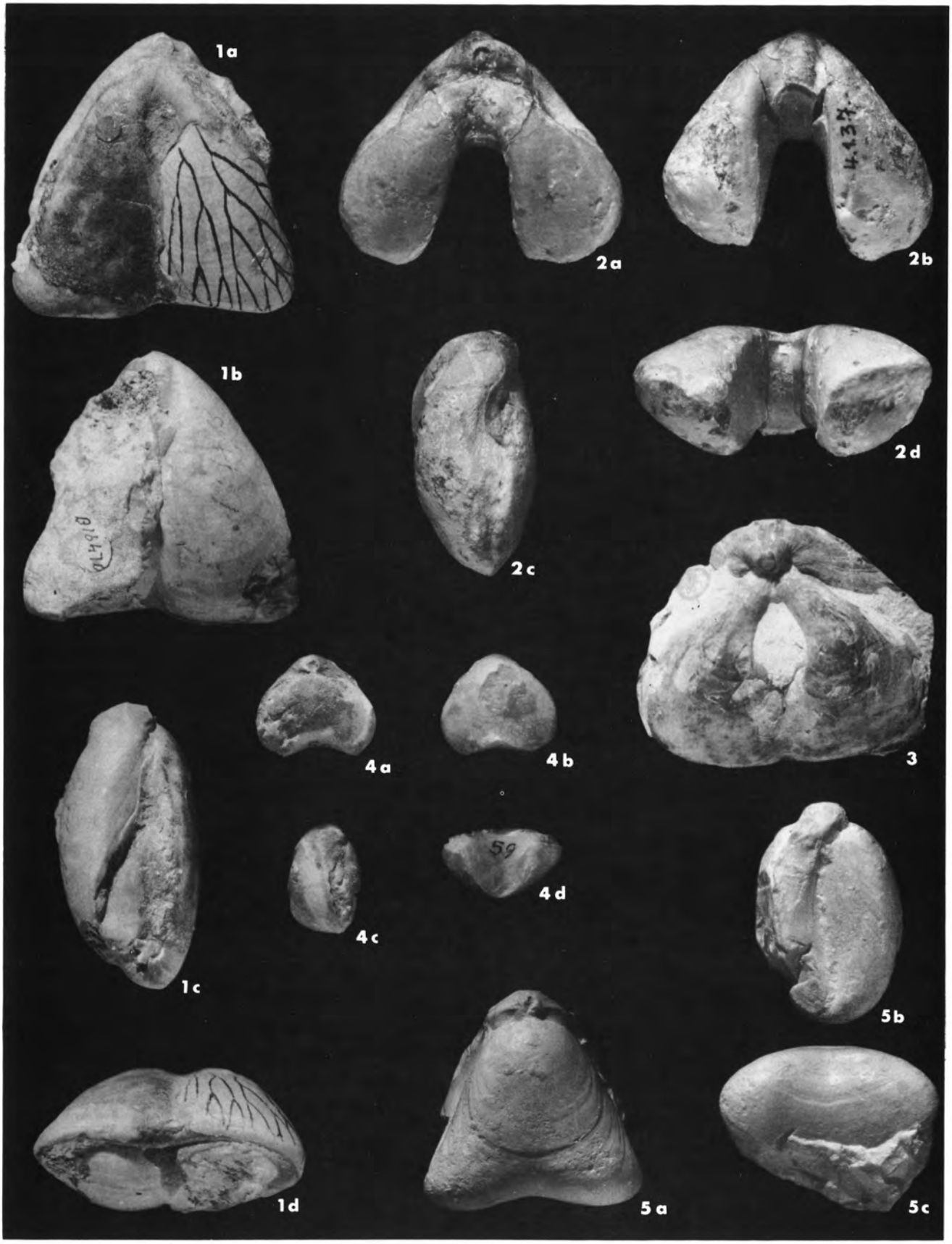
Description — Adult members of this species vary widely in thickness and hence in the sinuosity of the lateral commissure, increased thickness being correlated with increased sinuosity. The main variable character, however, is the shape of the lateral margins, which may be concave, gently convex or (rarely) straight. Commonly the lateral margins are concave and the anterior margin strongly curved backwards to meet them, so that the maximum width of the shell occurs about two thirds of the distance from posterior to anterior (P/A ratio: 2). Bruguière's original figure is of a specimen of this type and it is well shown by Jarre's « forme type moyenne » (Jarre 1962, fig. 5) and by pl. 1, fig. 3 herein. In some variants the concavity of the lateral margins is exaggerated and the junction of anterior and lateral margins occurs on laterally projecting protuberances of the shell; Parkinson's *T. triquetrus* shows this form, which is also exhibited by Jarre's « première variation », by Vogel's (1966) figured specimen and by pl. 1, fig. 1 herein.

Remarks — This species resembles *P. catulloi* in having the perforation more posterior than central, with the ventral perforation more posterior than the dorsal, but differs in being less extreme in these characters and in having a ventral perforation which is rounded triangular rather than semi-lunar. It differs also in general shape, being more rounded and less consistently triangular in ventral profile. *P. diphya*

EXPLANATION OF PLATE 4

Figs. 1 a-d - *Pygope catulloi* (Pictet). BM B 16470. « Diphya Kalk », Trento. Specimen referred by Buckman (1906, p. 442) to *Antinomia cor* (Bruguière) and considered by him to show a significant difference in the vascular markings from *Antinomia catulloi* (see Plate 3, fig. 3).
Figs. 2 a-d - *Pygope janitor* (Pictet). Museo di Storia Naturale, Rovereto, no. 4.1.3.7., Rosso Ammonitico, San Valentino.
Fig. 3 - *Pygites diphyoides* (d'Orbigny). IGP 663. Upper Valanginian (Biancone), Canove. De Zigno Coll. Specimen figured by Pictet (1867, pl. 29, fig. 1).
Figs. 4 a-d - *Nucleata planulata* (Zejszner). IGP 786. Tithonian (Rosso Ammonitico), Tresché. De Zigno Coll.
Figs. 5 a-c - *Triangope triangulus* (Valenciennes). IGP 10310. Upper Tithonian (Biancone), Bosco Chiesanuova. Plaster cast of sectioned specimen (see text-fig. 6).

All figures at natural size.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differs from both *P. janitor* and *Pygites diphyoides* in the position and size of the perforation and from *Pygites diphyoides* in the characters of the apical fold and sulcus.

There is room for doubt whether Colonna's (1606) figure represents this species. The ventral view seems to be depicting, and in fact emphasizing, a sulcus down the middle of the ventral apical fold, suggesting that the specimen was *Pygites diphyoides*. The dorsal view, on the other hand, does not show a median fold in the apical sulcus. Pictet (1867, pp. 138-39) considered this possibility but did not think the evidence good enough.

Distribution — There is no record of this species before the Tithonian. It is, however, abundant and characteristic in that stage in Algeria, Morocco, the Betic region of Spain, Majorca, the sub-Alpine chains of south-east France, Fribourg and central Switzerland, the north Italian Alps, western Sicily, the Polish Carpathians, the Bakony Forest and Gerecse Mountains (Hungary) and western Bulgaria. In the Carpathian region it continues into the Berriasian (Birkenmajer 1963) and Fallot (1922) recorded it as a rare species in the Neocomian of Majorca.

PYGOPE CATULLOI (Pictet, 1867)

Pl. 1, fig. 5; pl. 2, figs. 1-5; pl. 3, figs. 1-3; pl. 4, fig. 1. Text-fig. 4.

1792 *Terebratula cor* - BRUGUIÈRE, p. 425.
[1797] *Terebratula* - [BRUGUIÈRE], pl. 240, figs. 6a-c.
pars 1827 *Terebratula antinomia* - CATULLO, p. 169, pl. 5, fig. t (*non* p, q,r; ?s).
1829 *Terebratula antinomia* - CATULLO, p. 317, pl. 5, fig. 5.
1841 *Terebratula antinomia* - CATULLO, p. 237, pl. 2, fig. 2.
v 1851 *Antinomia dilatata* - CATULLO, p. 75, fig. 4.
v 1851 *Antinomia angulata* - CATULLO, p. 75, fig. 4.
v 1851 *Antinomia angusta* - CATULLO, p. 75, fig. 4.
1867 *Terebratula dilatata* Catullo - PICTET, p. 171, pl. 32, figs. 1-6; pl. 33, figs. 1-3.
\+ 1867 *Terebratula Catulloi* - PICTET, p. 202.
1871 *Terebratula diphya* von Buch - QUENSTEDT, p. 362, pl. 47, figs. 115, 119.
v 1906 *Antinomia dilatata* Catullo - BUCKMAN, p. 442, pl. 41, fig. 5.
v 1906 *Antinomia Catulloi* (Pictet) - BUCKMAN, p. 442.
1906 *Antinomia angusta* Catullo - BUCKMAN, p. 443, pl. 41, fig. 7.
v 1906 *Antinomia Quenstedti* - BUCKMAN, p. 443.
v pars 1907 *Terebratula (Pygope)diphya* Col. - DAL PIAZ, p. 152.
v 1962 *Pygope catulloi* (Pictet) - JARRE, p. 58, pl. D, figs. 4,5,6,9; pl. E, figs. 2,3.
1964 *Pygope dilatata* (Catullo) - HÖLDER, p. 166-167, text-fig. 47 (3a-b).
1964 *Pygope dilatata* (Catullo) - FÜLOP, pl. 12, figs. 2,4; pl. 24, fig. 1.
v 1965 *Antinomia catulloi* (Pictet) - MUIR-WOOD, p. 802, fig. 679 (3a-c).
1966 *Pygope catulloi* - VOGEL, pl. 38, fig. 1; pl. 39, fig. 3.
1966 *Pygope diphya catulloi* (Pictet) - GEYSSANT, p. 79, pl. 3, figs. 5a,b.

Lectotype (here chosen) — IGP 7117 (pl. 3, fig. 1), Rosso Ammonitico, Cesuna (Altipiano dei Sette Comuni, Vicenza). This is the better preserved of Catullo's two syntypes of *A. dilatata*. Since Pictet's name *T. Catulloi* was expressly a replacement name for *A. dilatata*, the type of *T. Catulloi* must be that of *A. dilatata*.

Dimensions of lectotype — L = 53.5 mm, W = 58,75 mm; pedicle valve damaged.

Paralectotypes — IGP 7106 A, Tithonian (Biancone), Durlo; Catullo's other syntype of *A. dilatata*.

IGP 7106, Cesuna; Catullo's holotype of *A. angusta*.

IGP 7108, Tithonian (Rosso Ammonitico), Cesuna, and IGP 7109 (pl. 2, fig. 3), ? Kimmeridgian (Rosso Ammonitico), Cesuna; Catullo's two syntypes of *A. angulata*.

IGP 2569, Tithonian (Biancone), Santa Giustina, Feltre, labeled *T. pseudodiphya* by De Zigno (ms).

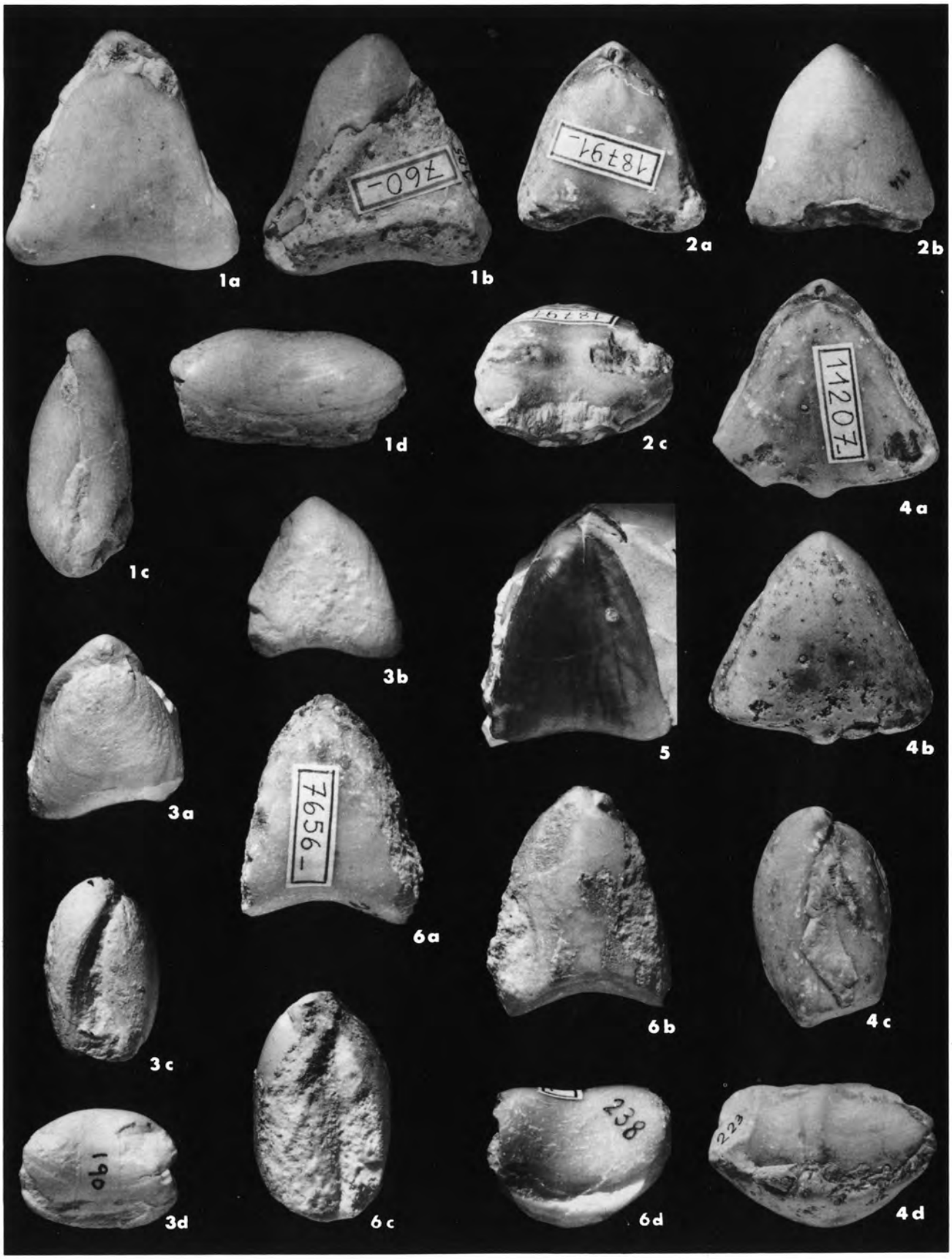
Material — 74 specimens from the Rosso Ammonitico and Biancone of the Venetian Alps (text- fig. 1).

Diagnosis — *Pygope* triangular in ventral profile,

EXPLANATION OF PLATE 5

Figs. 1 - 6 - *Triangope triangulus* (Valenciennes): 1 a-d) IGP 760. Upper Tithonian (Biancone), Sette Comuni. De Zigno Coll. A relatively thin variant. 2 a-c) IGP 18791. Biancone, Sette Comuni. A relatively thick variant. 3 a-d) IGP 16578. Tithonian (Biancone), Vette Feltrine. Plaster cast of sectioned specimen (see text-fig. 5). 4 a-d) IGP 11207. Tithonian (Rosso Ammonitico), Solagna. A specimen showing a central projection in the embayment of the anterior margin. 5) IGP 7135. Biancone, Pove di Bassano. Catullo Coll. To show the vascular markings of the brachial valve. 6 a-d) IGP 7656. Rosso Ammonitico, Torri del Benaco. A thick variant, showing development of a « linguiform extension ».

All figures at natural size.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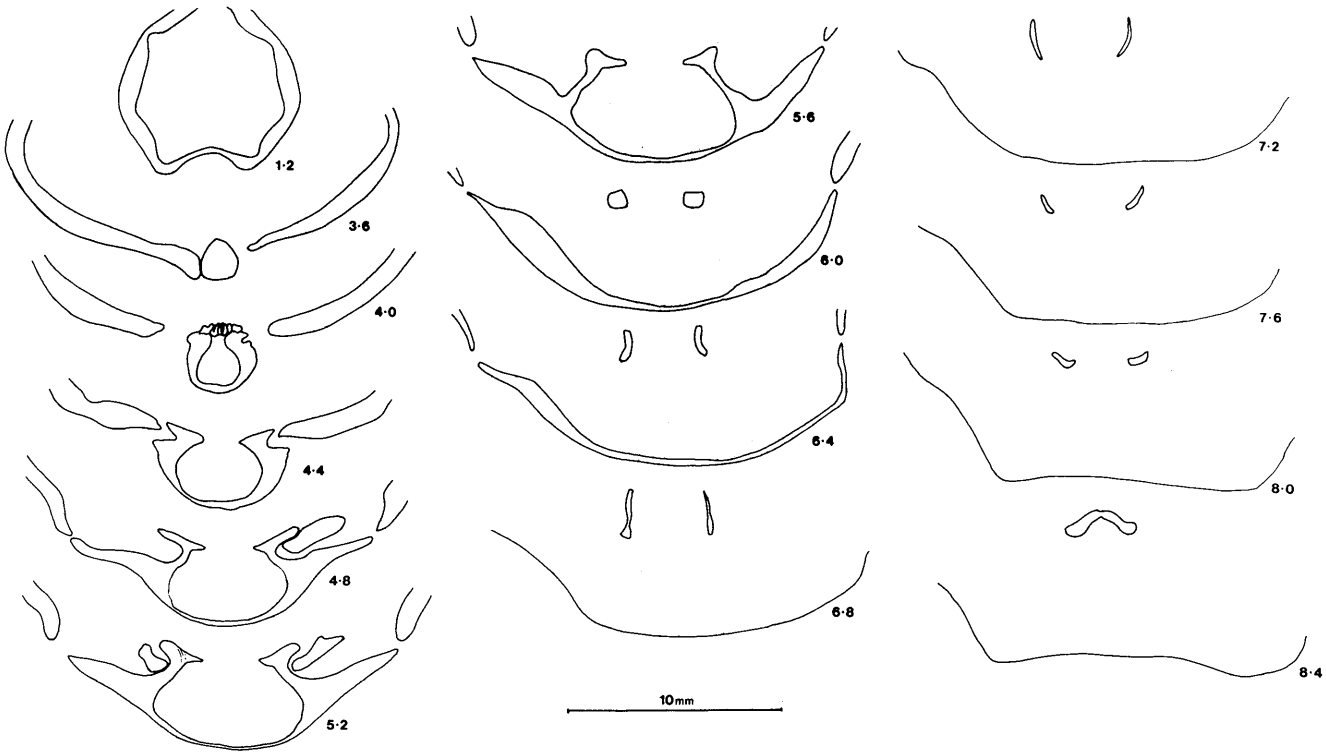
with centrally indented anterior margin. Dorsal perforation small, oval and close to the umbo; perforation tube curving obliquely ventralwards and posteriorwards so that the perforation in the pedicle valve is more posteriorly situated than that in the brachial valve; ventral perforation very small and semi-lunar in shape. Ventral apical fold bold and pronounced, oval in outline (« like a grain of rice », Pictet 1867, p. 171). Dorsal apical sulcus smooth, not clearly marked off from the general curve of the valve. Lateral commissure strongly sinuous. Anterior commissure more or less rectimarginate. Pedicle valve forms about two thirds of the anterior view. Mantle canal markings strong, closely spaced.

Description — The main variations in this species concern the width, the concavity or convexity of the lateral margins and the concavity of the anterior margin. Catullo's *A. angusta* represents a particularly narrow form, his *A. angulata* a morphotype in which the anterior parts of the lateral margins are convex and Bruguière's *T. cor* another morphotype in which the lateral margins are slightly convex throughout. Catullo's (1851) figure of *A. dilatata* depicts the extremely transverse shape, with concave lateral margins, which is found in some specimens (e.g. BM B38998). Buckman's *A. Questedti* consists of slightly thick variants.

Remarks — This species resembles *P. diphya* in having the perforation close to the posterior end and in the characters of the apical fold and sulcus, but differs from it in that (i) the perforation is even more distinctly posterior of the centre; (ii) the ventral perforation is very small and semi-lunar; (iii) the ventral apical fold is bolder and more pronounced; (iv) the



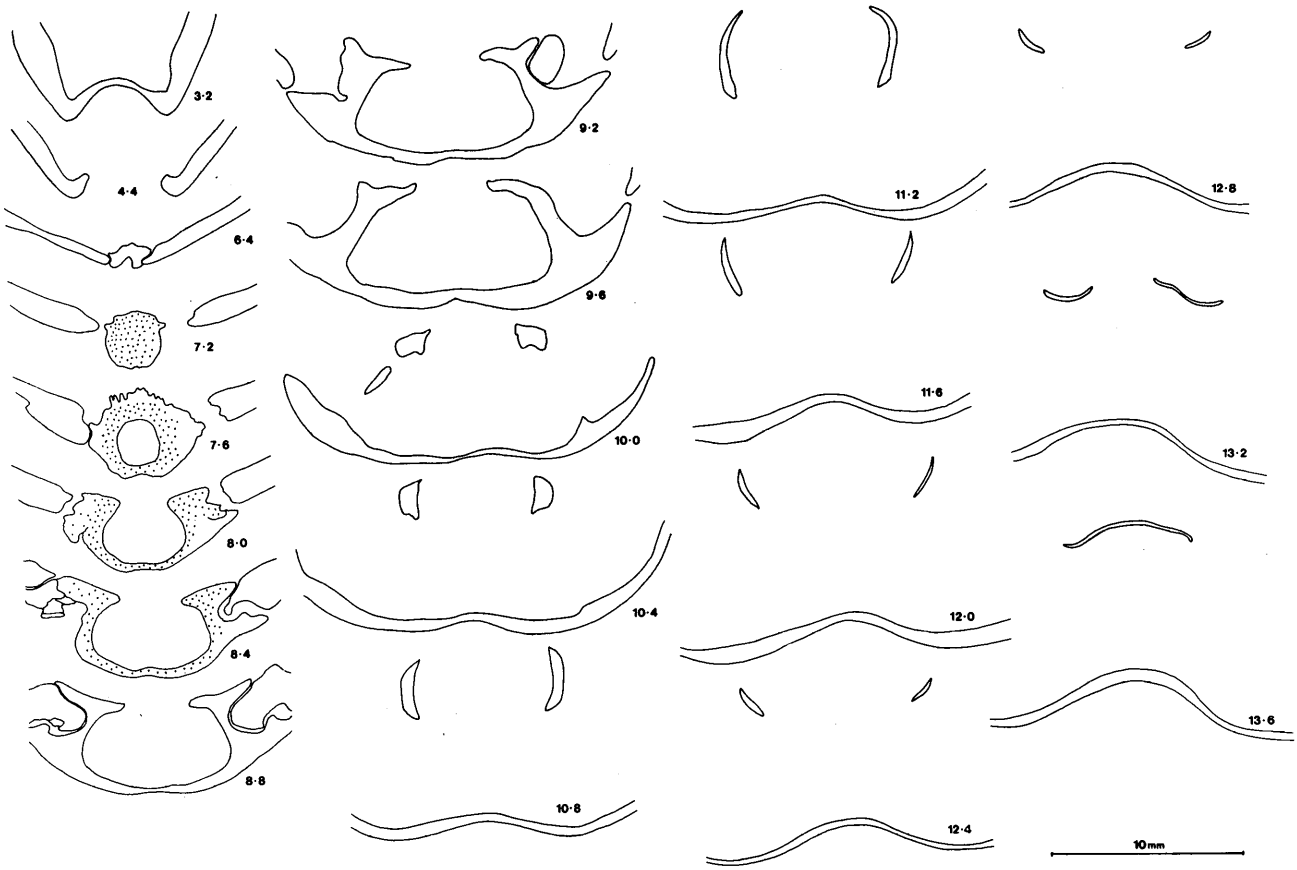
Text-fig. 3 - Transverse sections through *Pygope diphya.*
The narrow horizontal hinge plates, lacking attached crural bases, are seen in section 4.4 - 5.6; the rectangular free crural bases in 6.0; the maximum height of the crural processes in 6.8; the short loop and low-arched transverse band in 7.2 - 8.4.
IGP 12087, Tithonian (Biancone), Durlo (Monti Lessini).

shell in ventral profile is more consistently triangular, rounded morphotypes such as occur in *P. diphya* being not known; (v) the lateral commissure is more strongly sinuous.

P. catulloi differs from both *P. janitor* and *P. diphyoides* in the position and size of the perforation and from *P. diphyoides* in the characters of the apical fold and sulcus.

Distribution — This species has sometimes been stated to occur as early as the Oxfordian (Jarre 1962, Ager 1975). Ficheur (1890) claimed to have found it in the Ouarsenis Massif (Algeria) both below and above the occurrence of *Gregoryceras transversarium*. Bertrand (1891), puzzled by this occurrence, suggested that the strata might be inverted, which Ficheur (1891) categorically denied. Rèpelin (1895), however, proved inversion of the Jurassic in that region, although he did not find any specimens of *Pygope*. The subsequent field work of Dalloni (1936) and Calembert (1937, 1952) demonstrated the presence of pygopids only in the Tithonian, although they did not record this species. In the University of Padua collection a number of specimens of this species were labeled "Oxfordian". We have made thin sections of the matrices of five representative examples, all of which contained *Chitinoidella boneti* Doben, *Ch. cubensis* (Furrazola Bermudez) and *Ch. cristobalensis* (Furrazola Bermudez), indicating a Middle Tithonian to early Late Tithonian age. There is therefore no good evidence of the occurrence of this species before the Tithonian.

The species is particularly characteristic of the Tithonian of the north Italian Alpine area, where it is almost invariably closely associated with *P. diphya*. In Algeria there seems to have been no record of the species since Ficheur. Geyssant (1966) records it from the Tithonian of the Rif (northern Morocco) and Majorca. In the Betic region of Spain it occurs in all parts of the Tithonian including the Tithonian-Berriasian passage beds (Fallot 1931, 1934). It is known in the Ti-



Text-fig. 4 - Transverse sections through *Pygope catulloi*.
The narrow horizontal hinge plates, lacking attached crural bases, are seen in section 8.0 - 9.6; the rectangular free crural bases in 10.0; the maximum height of the crural processes in 11.2; the short loop and low-arched transverse band in 11.6 - 13.6. Stipple represents silicified skeletal tissue.
IGP 738, Tithonian (Rosso Ammonitico), Tresché (Sette Comuni).

thonian of Canton Fribourg and the Czorstyn-Rogoznik area of the Polish Carpathians.

In two areas the species apparently continues into the Lower Cretaceous. Kilian (1910) described from the Berriasian of St. Julien (Hautes-Alpes) a form transitional between *P. catulloi* and *P. diphya*. Jarre (1962, p. 64-65) redescribed this specimen and gave good reasons for ascribing it to *P. catulloi* as « var. *concava* ». Fülop (1964) records *P. catulloi* (as *P. dilatata*) from both Berriasian and Valanginian strata in the Bakony Forest.

The species has not been found up to now either in Sicily or in the Balkan region. *P. catulloi* thus occurs in association with *P. diphya* and seems to have a similar range in time but a more restricted geographical range.

PYGOPE JANITOR (Pictet, 1867)
Pl. 4, fig. 2

	1844	*Terebratula Duvalii* - NEWMAN, figs. a-d.
+	1867	*Terebratula janitor* - PICTET, p. 161, pl. 29, figs. 4-6; pl. 30, figs. 1-10.
	1885	*Terebratula (Pygope) janitor* Pictet - NICOLIS & PARONA, pl. 4, figs. 14-16.
	1906	*Pygope janitor* (Pictet) - BUCKMAN, p. 445, pl. 41, fig. 12.
v	1906	*Pygope Duvali* (Newman) - BUCKMAN, p. 446, pl. 41, fig. 14.
	1906	*Pygope* sp. - BUCKMAN, pl. 41, fig. 11.
	1960	*Pygope janitor* (Pictet) - SMIRNOVA, p. 376, pl. 2, figs. 3 a-d.
?	1960	*Antinomia diphya* (von Buch) - SMIRNOVA, p. 376, pl. 2, figs. 4a-d.
v	1962	*Pygope janitor* (Pictet) - JARRE, p. 38, pl. B figs. 2-5; pl. C, fig. 4 (*cum syn.*).
	1964	*Pygope janitor* (Pictet) - HÖLDER, p. 166-167, text-fig. 47 (4-5).
	1965	*Pygope deltoidea* (Valenciennes) - MUIR-WOOD, fig. 678 (1a-c).
	1966	*Pygope janitor* (Pictet) - GEYSSANT, p. 76, pl. 2, figs. 1-9.
	1972	*Pygope janitor* (Pictet) - SMIRNOVA, p. 64, pl. 5, figs. 2a-d.
	1976	*Pygope diphya* - AVRAM, pl. 10, fig. 15.
	1978	*Pygope janitor* - TSHUMACHENKO, pl. 4, fig. 1.

Serial sections are figured by Smirnova (1972).

Lectotype (chosen by Buckman 1906) — The specimen figured by Pictet (1867), pl. 30, fig. 2 bis, from Saint-Julian de Beauchêne (Lory Coll). This was an unfortunate choice, as Pictet indicated pl. 29, fig. 5 as the typical form from the type-locality of La Porte de France.

Material — One specimen from the Rosso Ammonitico of San Valentino, near Brentonico (prov. Trento), housed in the Museo di Storia Naturale, Rovereto.

Original description (translated from Pictet 1867, p. 161) — Shell subtriangular, with rounded angles, wide in the cardinal region. Sides straight or convex, ending towards the palleal region in angles which are little pronounced. These present two rounded curves. Greater valve moderately inflated, with a wide umbo giving rise to a massive rounded smooth fold, more or less projecting, and sometimes occupying nearly half the length of the shell. Perforation very large, its centre nearer to the palleal region than to the umbo, perforating the two valves directly so as to form a wide horizontal canal. Lesser valve incised, from its posterior end, by a strong triangular depression, without internal fold, which embraces the perforation as two ridges. Lateral commissure often occupying a furrow, almost straight in its posterior half and becoming somewhat sinuous by the curvature of the lesser valve, which presses into the greater valve. Greater valve showing feeble beak ridges which become rounded anteriorly as they approach the hinge. Lesser valve not carinate. Anterior commissure straight, both valves being thickened in that region. Foramen circular or oval, small.

Remarks — As discussed above (p. 24) there are specimens intermediate in character between *P. janitor* and *P. diphya*. One of these is the specimen from the Berriasian of La Faurie (Hautes Alpes) referred to by Jarre (1962, p. 45) (no. 1237 in the Grenoble Collection). In this the perforation is markedly nearer to the posterior end than to the centre of the shell but the

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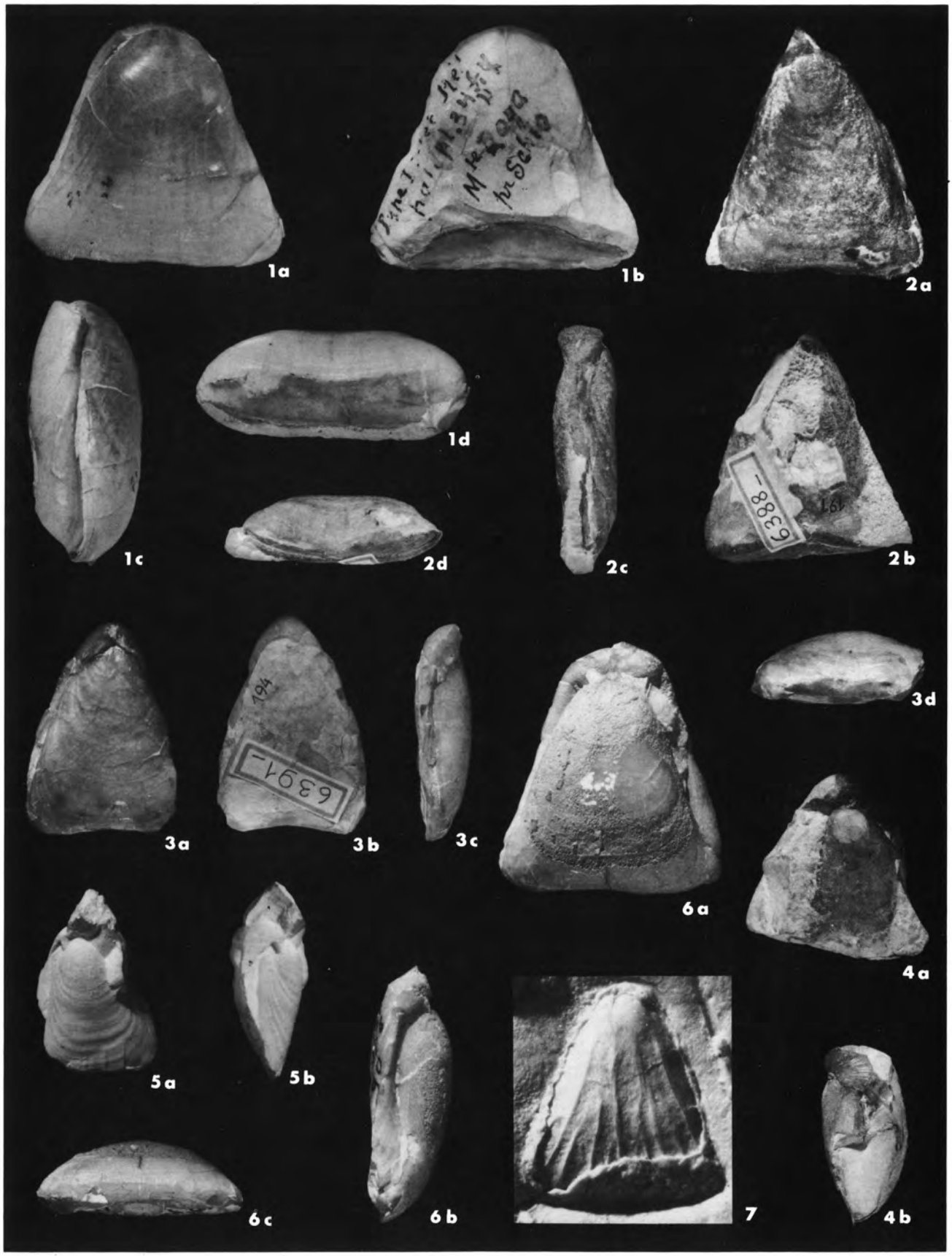
EXPLANATION OF PLATE 6

Figs. 1 a-d - *Triangope triangulus* (Valenciennes). Muséum d'Histoire Naturelle, Geneva (unnumbered). Monte Raga, near Schio. Specimen figured by Pictet (1867, pl. 34, fig. 7) and by Vogel (1966, pl. 38, fig. 2).

Figs. 2 - 7 - *Triangope euganeensis* (Pictet): 2 a-d) IGP 6388. Lower Cretaceous (Biancone), Monte Vignole (Teolo). De Zigno Coll. Lectotype. 3 a-d) IGP 6391. Lower Cretaceous (Biancone), Monte Vignole (Teolo). De Zigno Coll. Paralectotype. 4 a,b) IGP 6391A. Lover Cretaceous (Biancone), Monte Vignole (Teolo). Paralectotype. 5 a-b) IGP 6391B. Lower Cretaceous (Biancone), Monte Vignole (Teolo). Plaster cast of sectioned specimen (see text-fig. 7). 6 a-c) Muséum d'Histoire Naturelle, Geneva (unnumbered). Asiago. Syntype (fig. Pictet 1867, pl. 34, fig. 8). 7) IGP 6375. Lower Cretaceous (Biancone), Monte Vignole (Teolo). Rubber cast of brachial valve, to show vascular markings.

All figures at natural size.


1a
1b
2a
1c
1d
2d
2c
2b
3a
3b
3c
3d
6a
4a
5a
5b
6c
6b
7
4b

perforation tube is not oblique. Jarre (ms. label) at first regarded it as *P. diphya* but later, mainly because of the non-oblique tube, classified it as *P. janitor.*

Another five specimens at Grenoble (Arnaud Coll.) are from the Hauterivian of Les Granges, Romeyer-en-Diois; there is no doubt about their age (ammonites). These have the fold and sulcus characters of either *janitor* or *diphya,* but the perforation is definitely nearer to the posterior than to the centre and the perforation is slightly nearer to the posterior on the ventral side than on the dorsal side. Nevertheless, in view of the undoubtedly Hauterivian age, it seems easier to regard these as a late development of *P. janitor* than as a survival of *P. diphya.*

Distribution — This species has by far the longest range in time and the widest distribution in space among the perforate pygopines. There are persistent records in the literature of its occurrence in the *Hybonoticeras beckeri* Zone of the Upper Kimmeridgian in Ardèche, Voirons (east of Geneva), the Fribourg Alps, the Melchtal Alps and the Nagyhagymas Mountains (eastern Carpathians, eastern Transylvania). Geyssant (1966) summarizes these records.

In the Tithonian proper it occurs throughout the peri-Mediterranean Tethyan region: Sicily, Tunisia, Algeria, northern Morocco, south-eastern Spain, the Balearic Islands, south-eastern France, central Switzerland, the north Italian Alps, Štramberk, the Polish Carpathians, the Romanian Carpathians, the Belgrade area and north-west Bulgaria. In many of these areas it is definitely recorded in the lower part of the stage (south-east France, Savoy, central Switzerland, north-west Bulgaria, Tunisia) but in northern Italy, the Carpathians and Yugoslavia it seems to be commonest in the Upper Tithonian "Štramberk Limestone", that is somewhat later than the maximum abundance of *P. diphya* and *P. catulloi* in the Middle Tithonian "Diphya Limestone". This is the justification for Jarre's (1962) and Ager's (1979) recognition of a « zone » of *Pygope janitor* in the Upper Tithonian as distinct from a "zone" of *P. diphya* and *P. catulloi* in the Lower Tithonian.

The species continues into the Berriasian in Algeria (Bertraneu 1952, Dalloni 1952), south-eastern Spain (Fallot 1931), Ardèche and Hautes Alpes (Grenoble Coll.), the Voralberg-Upper Rhine region (Heim & Baumberger 1933) and possibly the Carpathians (Kotansky & Radwanski 1959 – with comment on this paper by Jarre 1962, p. 38).

In the Valanginian the species reached east Greenland (Donovan 1955, 1957; Owen 1976; Middlemiss 1979). There are specimens in the British Museum (Nat. Hist.) from the Hauterivian of Cheiron, near Castellane (Basses Alpes) (BM 6950, B 5003, B 6942). Geyssant (1966, p. 87) expresses surprise at Kilian's (1895) record of the species from the Barremian of Basses Alpes, but Karakash (1907) and Smirnova (1972) have figured specimens from the Lower Barremian of the Crimea.

Genus Pygites Buckman, 1906

Type species (by original designation) — *Terebratula diphyoides* d'Orbigny, 1849.

Original diagnosis — « A series of diphyoid Terebratuloids with the characters of *Pygope,* except that in the preperforate stage (onto- and phylogenetic) the dorsal valve carries an additional fold, and the ventral valve an additional sulcus ».

Buckman's use of the term « preperforate stage » here is unnecessary as the same characters are seen in the perforate stage. The ventral apical fold has a wide median depression which causes the ridge of the fold, in fact, to be double. In large gerontic specimens (length over 42 mm) the anterior end of this depression flattens out and even becomes slightly convex before it is truncated by the perforation. The dorsal apical sulcus correspondingly has typically a median fold which tends to fade out as it passes anteriorwards down into the perforation (as normally in the perforate forms, nearly all the lining of the perforation tube is formed from the dorsal valve). This additional dorsal fold is a less constant character than the additional ventral sulcus.

Terebratula sima Zejszner shows a similar well marked depression in the centre of the ventral apical fold and ridge in the centre of the dorsal apical sulcus during the juvenile, glossothyrid, stage of development (Siblik 1979, p. 58). Buckman's definition of *Pygites* would therefore strictly include this species. Buckman himself included it in *Antinomia* (Buckman 1906, p. 441). Some later authors have assigned it to *Antinomia* (Barczyk 1972), others to *Pygope* (Siblik 1979). Barczyk's specimen figured as a juvenile *Pygope diphya* (1972, pl. 4, fig. 1) shows the same characters and is perhaps better regarded as a juvenile *T. sima.*

Species included — *Pygites diphyoides* (d'Orbigny, 1849).

Range of the genus — Upper Tithonian to Lower Barremian.

Pygites diphyoides (d'Orbigny, 1849)

Pl. 4, fig. 3.

\+ 1849 *Terebratula diphyoides* - d'Orbigny, p. 87, pl. 509, figs. 6-9.

v 1867 *Terebratula diphyoides* d'Orb. - PICTET, p. 158, pl.29, figs. 1-3.
v 1962 *Pygope diphyoides* d'Orbigny - JARRE, p. 30, pl. A, figs. 1-8; pl. B, fig. 1 (*cum syn.*).

Serial sections are figured by Ager (1975), Middlemiss (1978) and Nekvasilová (1980).

Lectotype (chosen by Nekvasilová 1980) — d'Orbigny Coll. no. 5537, Mus. d'Hist. nat., Paris; from the Berriasian of Berrias (Ardèche). Fig. d'Orbigny, 1849, pl. 509, figs. 6-9.

Material — One specimen from the Valanginian or Hauterivian of Canove (Altipiano dei Sette Comuni, Vicenza) figured by Pictet (1867, pl. 29, fig. 1); IGP 663, De Zigno Coll.

Original description (translated from d'Orbigny 1849, p. 87) — Shell depressed, somewhat triangular, with very rounded angles, as wide as long, contracted in the cardinal region, very dilated and obtusely truncated in the palleal region, the sides convexly arched and shallowly excavate. Upper valve somewhat inflated, little arched, with short and incurved umbo from which originate two small folds separated by a sulcus. These folds, at first simple and later bordered on each side by a sulcus, extend, in adult specimens, as far as a hole which perforates the centre of the shell, anterior of which is a simple median sulcus. Lower valve provided, close to its umbo, with a median fold bordered by two sulci which extend as far as the perforation. Foramen circular, small. Lateral commissure nearly straight, as is the anterior commissure.

Remarks — The macrofossils in association with this specimen quoted by Pictet (1867, p. 160) indicate a Late Valanginian age [*Duvalia dilatata* Blainville, 1827), *D. lata* (Blainville, 1827), *Olcostephanus (O.) astierianus* (d'Orbigny, 1840)]; the microfossils in its matrix confirm this stratigraphic assignment [*Nannoconus bermudezi* Brönnimann, 1955, *N. globulus* Brönnimann, 1955, *N. steinmanni* Kamptner, 1931, *Calcicalathina oblongata* (Worsley, 1971) Thierstein, 1971, *Micrantholithus obtusus* Stradner, 1963, *Parhabdolithus embergeri* (Noel, 1958) Stradner, 1963, *Stephanolithion laffittei* Noel, 1969, *Conusphaera mexicana* Trejo, 1969, without Calpionellids and without *Nannoconus bucheri* Brönnimann, 1955].

Jarre (1962, p. 38) points out that late Hauterivian-Barremian specimens of the species show a weakening of the sulcus in the ventral apical fold and of the fold in the dorsal apical sulcus, characters cited as diagnostic of the species; the species, that is, approaches *P. janitor* in appearance during the Hauterivian. It must be noted, however, that the fold in the dorsal apical sulcus is not at any time a constant character. Many specimens in the British Museum (Natural History) from the Berriasian of Berrias and neighbouring areas are distinguishable from *P. janitor* only by the sulcus in the ventral apical fold.

Distribution — In first describing this species d'Orbigny (1849) stressed that it occurred only in the Neocomian, and this has been repeated by Pictet (1867) and Jarre (1962). Nevertheless, substantial claims have been made for its appearance in at least the Upper Tithonian. Roman (1950) records it from that stage in Ardèche, near Berrias and Vogué; Kilian (1895) from the Tithonian of the Montagne de Lure (Basses Alpes). Fallot (1931) lists it as occurring in the « pink Tithonian » of Barranco in south-east Spain but admits that the fauna in which it is found includes Berriasian elements. Castany (1955) even records it from the Lower Tithonian of Tunisia, which seems unlikely.

The species is most widespread in the Berriasian, being known in that stage in Algeria (Glaçon 1952), south-eastern Spain and Ibiza (Fallot 1922, 1931), and occurring abundantly in the Fosse Vocontienne region (Ardèche, Diois, Les Baronnies, Basses Alpes).

It continues into the Hauterivian in the area of the Fosse Vocontienne (Roman 1934) and is also known in the Valanginian of Vorarlberg (Heim & Baumberger 1933), the Bakony Forest (Fülop 1964) and northwest Bulgaria (BM specimens, Ager Coll.). It occurs in the Valanginian of northern Italy, but rarely (our specimen). There is also Nekvasilová's (1969, 1980) record of its occurrence in the « Lower Cretaceous » of Štramberk. Ooster (1863) figures good specimens from the « Cretaceous » of the Bernese and Vaudoise Alps. Jarre (1962, p. 35) considers that the latest known occurrences are Middle Hauterivian; Fülop (1964), however, figures it from the Lower Barremian of the Bakony Forest.

Genus TRIANGOPE nov.

Type species — *Terebratula triangulus* Valenciennes *in* Lamarck, 1819.

Diagnosis — Pygopinae with suberect to incurved umbo; foramen oval, permesothyrid; deltidium very small or invisible; beak ridges moderately sharp. Shell triangular, imperforate. Hinge plates slightly convex; crural bases given off dorsally from anterior ends of hinge plates.

Name — The name is derived from *Terebratula triangulus*.

Remarks — It has been argued above (p. 20) that the imperforate species here included in this genus represent a separate lineage from the perforate species.

There is no hint of a deeply sulcate glossothyrid stage or of a bifidate stage in their ontogeny or phylogeny. Internally the origin of the crural bases by dorsal outgrowth from the anterior ends of the hinge plates is different from all other pygopid species.

It is tempting to question whether these species really belong in the Pygopinae with the perforate *Pygope* and the glossothyrid *Nucleata* or whether they should be transferred to the Capillithyridinae (*). Growth-line evidence, for what it is worth, suggests that the early growth stages of these species are subcircular, biconvex or gently sulcate shells resembling the earliest growth stages of *Nucleata* before the glossothyrid stage begins. This suggests that they may have descended not from species of *Nucleata* but from forms ancestral to *Nucleata* which never developed the glossothyrid stage. In this respect they resemble the capillithyridins, but they are here excluded from the Capillithyridinae on the grounds of the great difference in the form of the foramen and deltidium, absence of shell ornament and difference in the origin of the crural bases from the anterior ends of the hinge plates. They are retained, at least for the time being, in the Pygopinae, partly because of the weight of palaeontological opinion, over nearly two centuries, that the perforate and imperforate forms belong together, but also because of the similarity in the distribution of the mantle canal markings in *Triangope* and *Pygope* (see pl. 3, fig. 3 and pl. 5, fig. 5).

Species included — *Terebratula triangulus* Valenciennes, 1819; *Terebratula euganeensis* Pictet, 1867.

Range of the genus — (Upper Kimmeridgian?) Lower Tithonian to Lower Barremian.

TRIANGOPE TRIANGULUS (Valenciennes, 1819)
Pl. 4, fig. 5; pl. 5, figs. 1-6; pl. 6, fig. 1.
Text-figs. 5-6.

1792 *Terebratula pileus* - BRUGUIÈRE, p. 424.
[1797] *Terebratula* - [BRUGUIÈRE], pl. 241, figs. 1a-c.
pars 1811 *Terebratulites triquetrus* - PARKINSON, p. 229, pl. 16, fig. 8 (*non* fig. 4).
v + 1819 *Terebratula triangulus* - VALENCIENNES *in* LAMARCK, p. 250, no. 21.
pars 1827 *Terebratula antinomia* - CATULLO, p. 169, pl. 5, fig. q (*non* figs. p,r,s,t,).
v 1829 *Terebratula mutica* - CATULLO, p. 316, pl. 5, fig. 4.
1834 *Terebratula triangulus* Lamarck - VON BUCH, p. 89.
1838 *Terebratula triangulus* Lamarck - VON BUCH, p. 197, pl. 18, fig. 10.
1841 *Terebratula mutica* Catullo - CATULLO, p. 238, pl. 2, fig. 4.
v 1850 *Terebratula triangulus* Valenciennes *in* Lamarck - DAVIDSON, p. 437, pl. 13, fig. 21.
? 1861 *Terebratula equicampestris* - GÜMBEL, p. 563.
? 1861 *Terebratula subtriangulata* - GÜMBEL, p. 563.
1867 *Terebratula triangulus* Lamarck - PICTET, p. 180, pl. 34, figs. 1-3.
v pars 1867 *Terebratula euganeensis* - PICTET, pl. 34, figs. 7a,b (*non* figs. 5,6,8,9,10).
1871 *Terebratula misilmerensis* - GEMMELLARO, p. 5, pl. 1, figs. 6-7.
1871 *Terebratula triangulus* Lamarck - QUENSTEDT, p. 367, pl. 48, figs. 9-11.
v 1906 *Antinomia pileus* (Bruguière) - BUCKMAN, p. 444, pl. 41, figs. 8a-c.
1906 *Pygope* (?) *subtriangulata* (Gümbel) - BUCKMAN, p. 448.
v 1907 *Terebratula (Pygope) Euganeensis* Pict. - DAL PIAZ, p. 152.
v 1907 *Terebratula (Pygope) triangulus* Lmk - DAL PIAZ, p. 150, 152.
v 1910 *Terebratula triangulus* Valenciennes in Lamarck - CLERC & FAVRE, pl. 5, figs. 22a-d.
1936 *Pygope triangulus* Lamarck - ROMAN, pl. 4, fig. 23.
1938 *Pygope triangulus* Lamarck - GOČANIN, pl. 1, fig. 9.
v 1962 *Pygope triangulus* (Lamarck) - JARRE, p. 70, pl. E, fig. 4; pl. F, figs. 1-6.
1964 *Pygope triangulus* (Lamarck) - FÜLOP, pl. 15, figs. 4a-c; pl. 25, figs. 3a,b.
1964 *Pygope triangulus* (Lamarck) - FÜLOP, pl. 15, figs. 4a-c; pl. 25, figs. 3a,b.
v 1966 *Pygope euganeensis* (Pictet) - VOGEL, pl. 38, fig. 2; pl. 39, fig. 2.
1966 *Pygope triangulus* - VOGEL, pl. 39, fig. 2.
1966 *Pygope triangulus* (Lamarck) - GEYSSANT, p. 79, pl. 1, figs. 7a-d.
1976 *Pygope triangulus* - FÜLOP, p. 34, figs. 8,9.

Holotype — Lamarck's specimen of *T. triangulus*, fig. Clerc & Favre 1910, pl. 5, figs. 22a-d. The specimen is in the Muséum d'Histoire Naturelle at Geneva.

Dimensions of holotype — L = 37,25 mm, W = 30.5 mm, T = 21.75 mm.

Material — 97 specimens from the Rosso Ammonitico and the Biancone of the Venetian Alps (text-fig. 1).

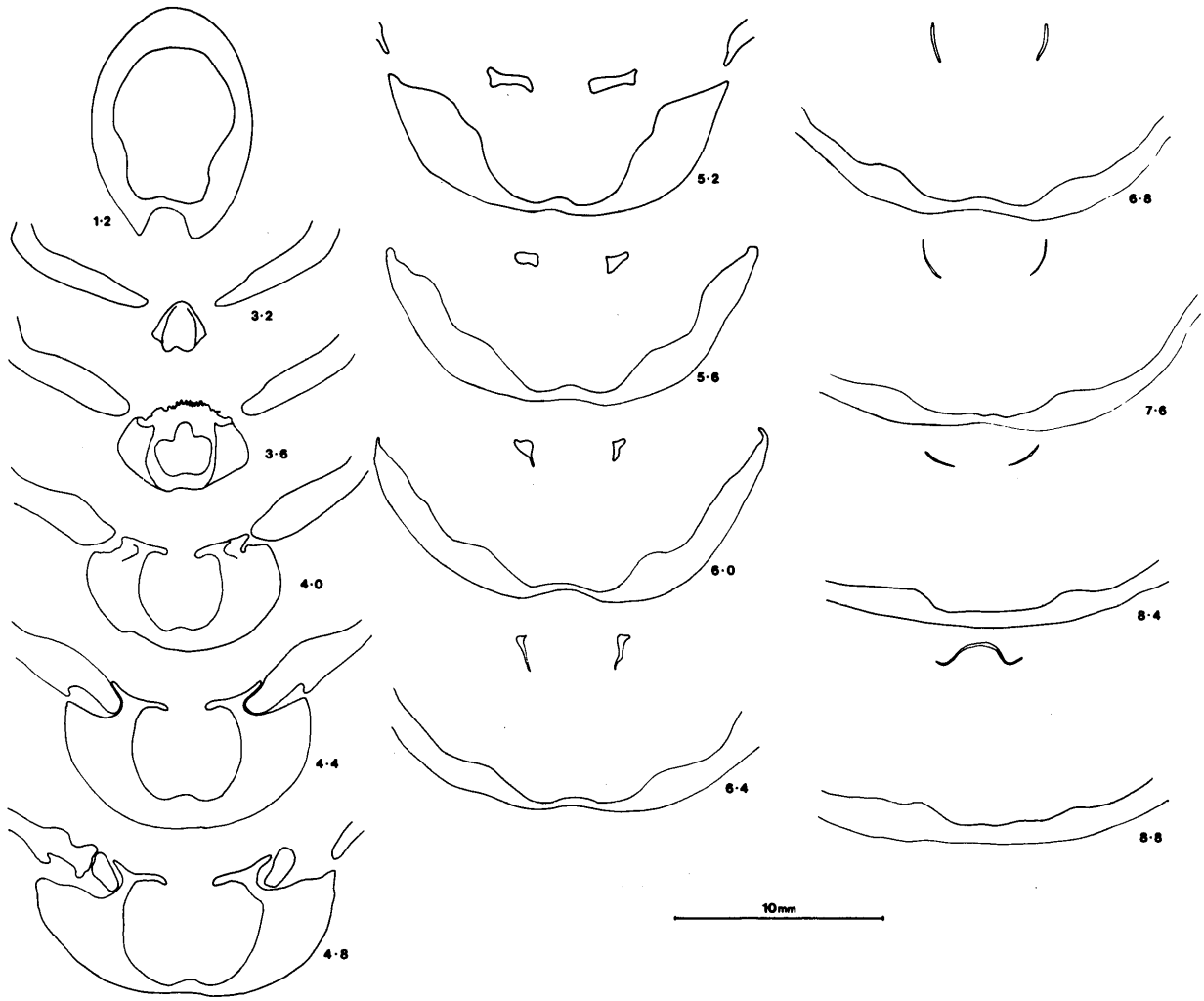
Diagnosis — *Triangope* triangular or rounded triangular in ventral profile; anterior margin strongly or gently indented, or doubly indented with central projection. Lateral regions of shell compressed, with lateral commissure occupying a furrow between the valves; lateral commissure slightly to markedly sinuous. Anterior commissure broadly sulcate, with brachial valve occupying much the greater part of the anterior view.

Description — There is considerable variation in the length/width and length/thickness ratios, in the

(*) Cowen (1981) has shown that *Platythyris* and Platythyridinae are invalid under the Law of Homonymy and should be replaced by *Capillithyris* and Capillithyridinae.

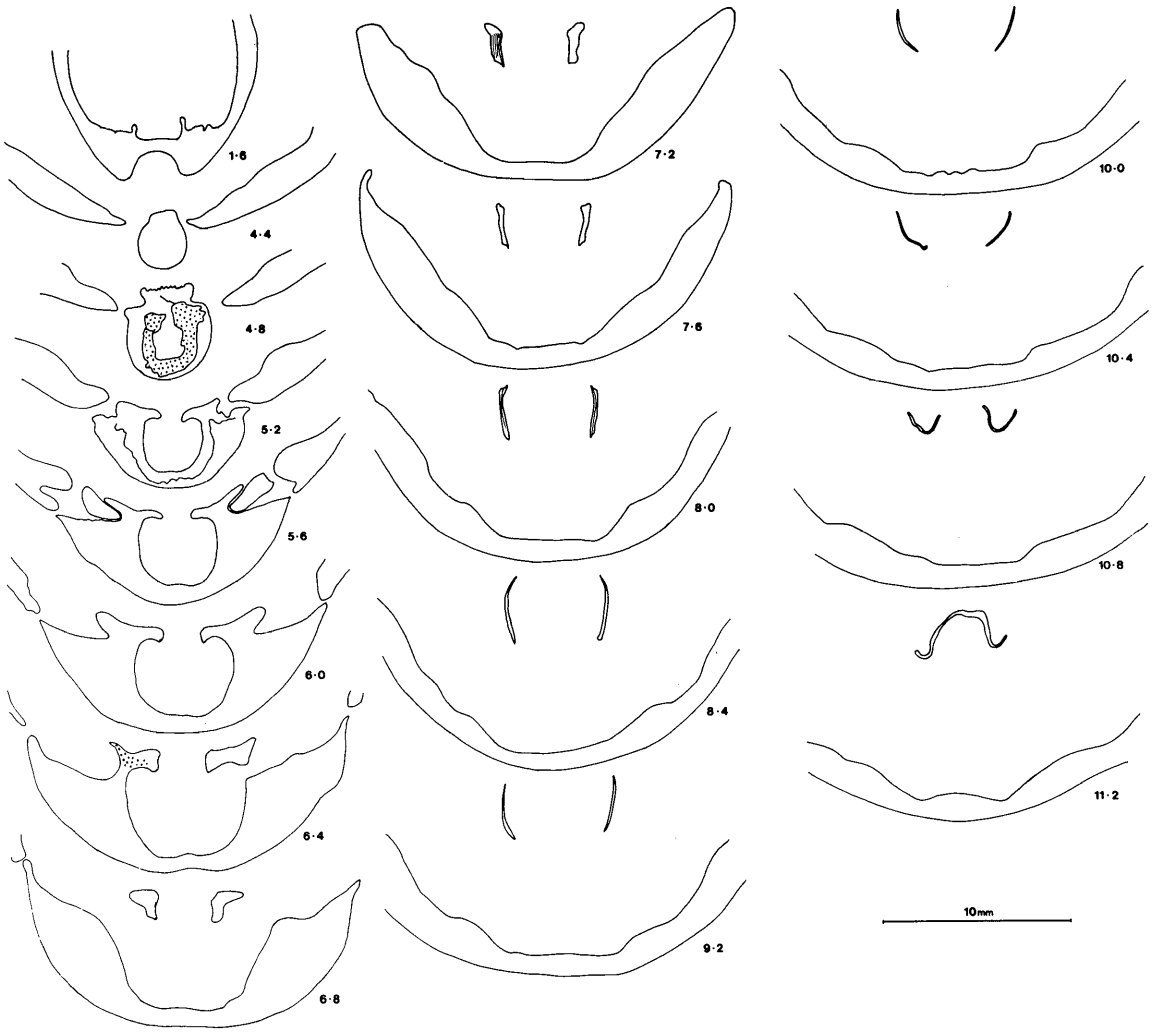
convexity or concavity of the lateral margins and the degree of embayment of the anterior margin. Jarre's (1962) plate F shows these variations well. This plate is misleading, however, in giving the impression that there is usually a deep straight median longitudinal groove running the length of the brachial valve, comparable to that shown by *Pygope catulloi* and *P. diphya;* such a character is not present in any of the well over one hundred specimens which we have been able to examine. There may or may not be a broad gentle longitudinal depression in the brachial valve.

The sinuosity of the lateral commissure varies in general with the relative thickness, as in *P. diphya.* Bruguière's original figure was of a variant with a deeply indented anterior margin. Relatively thicker specimens may have an anterior margin as indented as this or straighter; in individuals which combine relative thickness with an indented anterior margin, the combination of these characters with the characteristic ventralward inflexion of the anterior part of the brachial valve, to form nearly all of the anterior view, gives rise to a structure similar to the linguiform extension of rhynchonellids and of *Nucleata,* as pointed out by Buckman (1906, p. 453) (pl. 5, fig. 6 herein). In rare specimens the anterior face of the brachial valve may have a narrow projection subdividing the embayment (pl. 5, fig. 4); in some cases the subdivision is asymmetric, the projection not being central.



Text-fig. 5 - Transverse sections through *Triangope triangulus.*
The slightly convex hinge plates, lacking attached crural bases, are seen in sections 4.0 - 4.8; the subrectangular free crural bases in 5.6; in sections 5.2 - 6.4 the crura are seen to be given off dorsally from the anterior ends of the hinge plates; maximum height of the crural processes is seen in section 6.8; the short loop and low-arched transverse band in 7.6 - 8.8.
IGP 16578, Tithonian (Biancone), Vette Feltrine (Alpi Feltrine).

Remarks — Jarre (1962) attaches great importance to the anterior view, in which the brachial valve appears to form almost the whole thickness of the shell, a character which in his opinion is « la pierre de touche de l'espèce ». In particular, he regards this character as a criterion of differentiation from "*Pygope*" *rectangularis* (Pictet), but in fact in some of Jarre's specimens of "*P.*" *rectangularis* at Grenoble the brachial valve decidedly dominates the anterior view, while in some labeled *P. triangulus* the brachial and pedicle valves share the anterior view almost equally. The other main points of distinction between the two species are the more rectangular ventral profile, more depressed shell and straighter lateral commissure of "*P.*" *rectangularis*. As stated above, in *T. triangulus* there is a correlation between more depressed form and straighter lateral commissure. The morphological distinction between these two species is very indefinite and as they share the same stratigraphical range it is difficult not to regard "*P.*" *rectangularis* as merely a shape variant of *T. triangulus*. If "*P.*" *rectangularis* is a distinct species it must be a rare one as Pictet knew only three specimens, Mariani (1900) only one, Jarre only five, while it is not mentioned by Geyssant (1966). The variant (or species) *rectangularis* seems to be confined to the Tithonian of the Alps between Lombardy and Vienna, apart from Jarre's specimens, which are from the Berriasian of south-east France [although



Text-fig. 6 - Transverse sections through *Triangope triangulus*.
The slightly convex hinge plates, lacking attached crural bases, are seen in sections 5.2 - 6.4; in sections 6.4 and 6.8 the crura are seen to be given off dorsally from the anterior ends of the hinge plates; maximum height of the crural processes is seen in section 8.4; the short loop and low-arched transverse band in 9.2 - 11.2. Stipple represents silicified skeletal tissue.
IGP 10310, Upper Tithonian (Biancone), Bosco Chiesanuova (Monti Lessini).

Fülop (1976) records a specimen from the Tithonian of Tata, Hungary]. It is not represented in the Padua Collection.

Distribution — *T. triangulus* was claimed by Dal Campana (1904) to occur in the «Strati ad *Aspidoceras acanthicum* » at Collalto di Pove (Bassano), and there are in the Padua collection five specimens labeled « Kimmeridgian », from Altipiano dei Sette Comuni, Lamon and Torri del Benaco. Of these one, from Lamon, has been shown by the presence of *Polycostella beckmanni* Thierstein in its matrix to be Tithonian (probably Lower to Middle, because of the absence of *Chitinoidella*); another, from Torri del Benaco, contains *Chitinoidella dobeni* Borza in its matrix and is Middle Tithonian to basal Upper Tithonian. It is probable that all five specimens are, in fact, Tithonian. Nowak (1976) records it from « below the *Parastomiosphaera malmica* Zone » in the Polish Carpathians (the *Malmica* Zone being Lower Tithonian) but makes it clear (p. 117) that this could still be within the Lower Tithonian and not necessarily Kimmeridgian.

The Tithonian was its period of greatest abundance, when it is found in Algeria (red nodular limestones of Djudjura – Roman 1936), northern Morocco (Geyssant 1966), south-eastern Spain (Kilian 1889, Fallot 1934), Majorca (Fallot 1922), northern Italy (Nicolis & Parona 1885, Mariani 1900, Dal Campana 1904, Dal Piaz 1907), the Apennines of Marche and Umbria (Zittel 1869, Principi 1921), Sicily (Gemmellaro 1871), the north-east Alps (Trauth 1948), Carpathians, Hungary (Fülop 1976) and western Greece (references in Geyssant 1966). In the "Hierlatz facies" of the Lower Tithonian of the Gerecse Mountains, Hungary, Vigh (1961) records « almost a lumachelle » of *T. triangulus* and *P. janitor*.

The species remains abundant in the Berriasian, especially of south-east France (where it does not seem to be recorded in the Tithonian). There are numerous specimens at Grenoble from the Berriasian of the Diois, Les Baronnies and Basses-Alpes. Fallot (1922) records it as a rare species in the Neocomian of Majorca. It occurs in the Tithonian-Cretaceous passage beds of Lombardy (Mariani 1900), the « Neocomian » marls of the north-east Alps (Trauth 1948), the « Lower Neocomian » of the Bavarian Alps (Gümbel 1861) and the Berriasian of Hungary (Fülop 1976). It continues into the Valanginian near Belgrade (Gočanin 1938) and one specimen in the Padua collection, from the Biancone of Asiago (Sette Comuni), has been dated by the microfossils in its matrix to the Late Valanginian (no calpionellids and the same species as those listed on p. 39). Finally Fülop (1964) figures the species from the Lower Barremian of the Bakony Forest.

TRIANGOPE EUGANEENSIS (Pictet, 1867)

Pl. 6, figs. 2-7. Text-fig. 7.

v pars +	1867	*Terebratula euganeensis* - PICTET, p. 182, pl. 34, figs. 5,6,8,9,10 (*non* figs. 7a,b).
	1906	*Pygope* (?) *euganeensis* (Pictet) - BUCKMAN, p. 448, pl. 41, fig. 16.
v non	1907	*Terebratula* (*Pygope*) *Euganensis* Pict. - DAL PIAZ, p. 152.
v	1962	*Pygope euganeensis* (Pictet) - JARRE, p. 78, pl. H, figs. 1-4.
v non	1966	*Pygope euganeensis* (Pictet) - VOGEL, pl. 38, fig. 2.

Lectotype (chosen by Buckman 1906, p. 448) — IGP 6388, Biancone, Monte Vignole, near Teolo, Euganean Hills. Fig. Pictet 1867, pl. 34, fig. 5.

Dimensions of lectotype — L = 43 mm, W = 36 mm, T = 11.75 mm.

Paralectotypes — IGP 6391, fig. Pictet 1867, pl. 34, fig. 6; IGP 6391A, fig. Pictet 1867, pl. 34, fig. 10. Both from same locality and horizon as lectotype.

Material — 9 specimens from the type locality (see above), including three of Pictet's figured specimens. The originals of Pictet's figs. 7 and 8 are in the Muséum d'Histoire Naturelle at Geneva.

Original description (translated from Pictet 1867, p. 183) — Shell imperforate, in the form of a regular isosceles triangle, depressed, with almost straight sides and pointed posterior end. Umbo less incurved than in the preceding species (*diphyoides, janitor, diphya, dilatata, sima, triangulus, rectangularis*), without interarea, the sides of the umbo inturned and leaving a triangular space for a small deltidium, which appears to be missing. Valves flat, without sulcus or carena, smooth, marked by growth lines which are more apparent on the sides and trace out the triangular form of the shell. Anterior angles somewhat rounded. Palleal margin slightly indented. Lateral commissures straight. In anterior view the dorsal valve slightly covers the ventral valve.

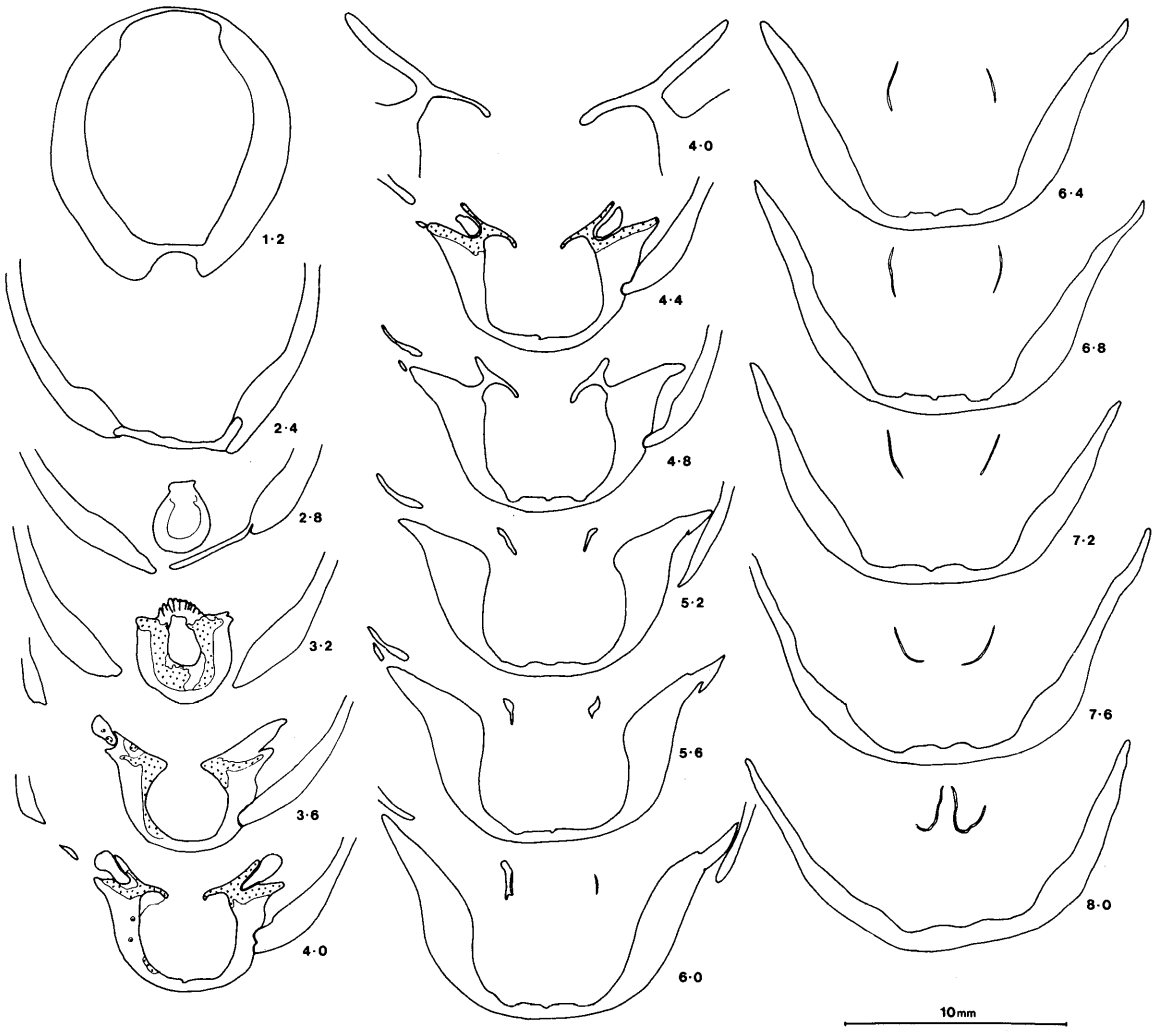
Emended diagnosis — *Triangope* of isosceles triangle outline in ventral profile; anterior margin straight or only slightly indented. Shell depressed, without any marked fold or sulcus. Lateral commissure straight or gently curved, not occupying a furrow. Umbo suberect to erect; deltidium very small but may be visible. Growth lines usually well-marked.

Remarks — This is a rare species; there are only three in the Grenoble Collection used by Jarre and only nine in the Padua Collection, some of which are dubious.

Jarre has doubts about the separation of this species from *T. triangulus* (Jarre 1962, p. 80) because of the variability in thickness shown by Pictet's figured specimens, which is greater than Pictet indicates in his text. Of Pictet's figures (1867, pl. 34), fig. 7 certainly appears to have all the characters of *T. triangulus*. The specimen (which is in the Musèum d'Histoire Naturelle at Geneva) was also figured as *P. euganeensis* by Vogel (1966); it is here excluded from the species and referred to *T. triangulus* (see plate 6, fig. 1 herein).

T. euganeensis is here retained as a separate species because its straight lateral and anterior margins, depressed form, beak less incurved and foramen more circular than in *T. triangulus*, and thinner hinge plates are distinctive morphological characters.

Distribution — Pictet, in describing this species, was convinced that it was confined to the Lower Cretaceous. Jarre repeats this. There are, however, several records in the literature of its occurrence in the Upper Tithonian. Trauth (1948) cites a « *Pygope euganeensis - triangulus* » from the Upper Tithonian of the north-east Alps; Fallot (1934) «*P. Euganeensis*» from the Upper Tithonian of the northern slope of the Sierra de Castillones in south-east Spain; Nicolis & Parona (1885) « *Terebratula Euganensis* » from the Up-



Text-fig. 7 - Transverse sections through *Triangope euganeensis*.
The thin, slightly convex hinge plates, lacking attached crural bases, are seen in sections 3.6 - 4.8; in sections 4.8 - 5.6 the crura are seen to be given off dorsally from the anterior ends of the hinge plates; maximum height of the crural processes (slightly damaged) is seen in section 6.4; the short loop and low-arched transverse band (damaged in this specimen) in 6.8-8.0. Stipple represents silicified skeletal tissue. Section 4.0 is enlarged to show the shape of the hinge plates.
IGP 6391 B, Lower Cretaceous (Biancone), Monte Vignole (Colli Euganei).

per white Tithonian of the Province of Verona; Dal Piaz (1907) « *Terebratula (Pygope) Euganensis* » from the Upper Tithonian of the Feltrine Alps (but we have re-examined these specimens, which are in the Padua collection, and refer them to *P. triangulus*); Mariani (1900) « *Pygope euganensis* » from the Tithonian (« rosso ad aptici ») of the Lesse Valley. In view of the rarity of the species and the difficulty of separating it from *T. triangulus* it would seem reasonable to take all these records as referring to *T. triangulus,* with the exception of Nicolis and Parona whose record is accompanied by a figure which certainly appears referable to Pictet's species.

It is essentially a local species in northern Italy, from the Lower Cretaceous of which it is recorded by Pictet and by Mariani (Maiolica of Campora and the Lesse Valley, in the Lombardian Alps, and the Biancone of the Venetian Alps), and also occurs rarely in the grey Neocomian limestone of the central Apennines (Principi 1921). Fallot (1922) records it as a rare species in the Neocomian of Majorca (without figure) and Fülop (1976) lists one specimen from the Berriasian of Tata, Hungary.

The associated macrofossils and the microfossils contained in the matrix of four paralectotypes and topotypes in the Padua collection have yelded ages from Late Berriasian – earlier Valanginian [*Calpionellopsis oblonga* (Cadisch, 1932), *Calpionellopsis simplex* (Colom, 1939), *Lorenziella hungarica* Knauer & Nagy, 1964, *Remaniella cadischiana* (Colom, 1948), *Tintinnopsella longa* (Colom, 1939), *Tintinnopsella carpathica* (Murgeanu & Filipescu, 1933), « *Calpionella* aff. *alpina* Lorenz, 1902 » *sensu* Allemann & Remane 1979] to Late Valanginian [*Duvalia dilatata* (Blainville, 1827), *Nannoconus broennimanni* Trejo, 1959, *N. colomi* (Lapparent, 1931) Kamptner, 1938, *N. steinmanni* Kamptner, 1931,*Calcicalathina oblongata* (Worsley, 1971) Thierstein, 1971, *Micrantholithus obtusus* Stradner, 1963, *Parhabdolithus embergeri* (Noel, 1958) Stradner, 1963, *Stephanolithion laffittei* Noel, 1956, *Conusphaera mexicana* Trejo, 1969, without Calpionellids and without *Nannoconus bucheri* Brönnimann, 1955].

Genus NUCLEATA Quenstedt, 1868

1868 *Nucleata* - QUENSTEDT, p. 25.
1879 *Glossothyris* - DOUVILLÉ, p. 267.

Range of the genus — (? Middle Jurassic) Upper Jurassic to uppermost Albian.

NUCLEATA PLANULATA (Zejszner, 1846)
Pl. 4, fig. 4.

\+ 1846 *Terebratula planulata* - ZEJSZNER, p. 24, pl. 2, figs. 13-17.
1870 *Terebratula planulata* Zeuschner - ZITTEL, p. 135, pl. 14, figs. 3-5.
1906 *Antinomia planulata* (Zeuschner) - BUCKMAN, p. 441, pl. 41, fig. 1.
1962 *Glossothyris planulata* (Zeuschner) - JARRE, p. 101, text-fig. 10, pl. J, fig. 5.
1972 *Nucleata planulata* (Zejszner) - BARCZYK, p. 156, text-fig. 5, pl. 1, figs. 4-5.

Holotype — The specimen figured by Zejszner 1846, pl. 2, figs. 13-17, from Rogóznik.

Material — 7 specimens from the Rosso Ammonitico of the Vette Feltrine and of Treschè and from the Biancone of the Verona district.

Description (shortened from Barczyk 1972, p. 156-157) — Shell biconvex, transverse-oval in outline. Maximum width in the region of anterior commissure. Width-length ratio 110 to 115. Pedicle valve more convex than brachial. Maximum thickness of shell somewhat below a point halfway its length. Thickness-length ratio 72. A single, wide fold, starting near cardinal margin, gradually deepening as it passes through the anterior commissure and forming a deep, lingulate sinus occurs on brachial valve. Anterior commissure sulcate, very strongly bent towards pedicle valve and shaped like a widely open letter U.

A lingulate bend of brachial valve projects above the greatest convexity of shell. Umbo short, robust, perdeject, strongly incurved over brachial valve. Lateral commissures substraight. Pedicle foramen small, situated on beak, mesothyrid. Cardinal margin arcuate.

Cardinal process small with a distinct myophore. Hinge plates straight, fused with crural bases. Crural processes long, straight. Brachidium composed of very short and narrow descending branches connected by a fairly strongly arcuate transverse band.

Distribution — *N. planulata* has been recorded only from the Tithonian and Berriasian of the southern Polish Carpathians (Barczyk 1972). There seems considerable doubt, however, whether the species can be clearly distinguished from *N. rupicola* (Zittel), which was recorded by Nicolis & Parona (1885) from the Tithonian of the Verona district, or even from *N. bouei* (Zejszner) which has been recorded by several authors from Kimmeridgian to Lower Cretaceous strata in northern Italy.

ACKNOWLEDGEMENTS

We are grateful to Dr. L. Altichieri (Museum of the Institute of Geology, University of Padua) and to Mr. E.F Owen (British Museum, Natural History) for access to specimens in their care and for the loan of specimens; to Monsieur J-P. Thieuloy for access to the collection of Pygopidae at the Institut Dolomieu (University of Grenoble) and to Monsieur L. Arnaud (Grenoble) for showing us specimens of his

own collection; to Dr. E. Lanterno (Muséum d'Histoire Naturelle, Geneva) for supplying plaster casts and photographs of Lamarck and Pictet type-specimens; to Dr. W. Barczyk (University of Warsaw) for allowing inspection of his collection of pygopids from the Pieniny Klippen Belt; to Dr. Gertruda Biernat (Polish Academy of Sciences, Warsaw) for her efforts, although unsuccessful, to trace the type specimen of *Pygope solidescens*; to Mr. R.V. Melville (International Commission on Zoological Nomenclature) for his expert advice on nomenclatural problems.

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