Palaeogeography, Palaeoclimatology, Palaeoecology, 100 (1993): 189-207
Elsevier Science Publishers B.V., Amsterdam

First record of Jurassic nucleatid brachiopods from the southwest Pacific with comments on the global distribution of the group

Miguel O. Manceñido
Division Paleozoologia Invertebrados, Museo de Ciencias Naturales, Paseo del Bosque, 1900 La Plata, Argentina

(Received January 24, 1991; revised and accepted August 20, 1992)

ABSTRACT

Manceñido, M.O., 1993. First record of Jurassic nucleatid brachiopods from the southwest Pacific with comments on the global distribution of the group. Palaeogeogr., Palaeoclimatol., Palaeoecol., 100: 189–207.

The global distribution of the brachiopod genera *Linguithyris*, *Nucleata*, *Phymatothyris*, *Securithyris* and *Triangope* is reviewed stratigraphically. From the Early Jurassic to the Late Cretaceous, they show a persistent fidelity to Tethyan areas, but for brief extensions elsewhere. Prominently among these, two fundamental new records are revealed: *Linguithyris agerorum* n. sp. from upper Liassic deposits of New Zealand (western coast of North Island), and *Nucleata* ex gr. *bouei*/*planulata* (Zeuschner) from the Upper Jurassic of Indonesia (the Sula Islands).

Taxonomical relationships are discussed and an updated classification is outlined, resulting in removal of *Phymatothyris* from the incertae sedis condition to be placed in the subfamily Nucleatinae, and, at a broader scale, it is proposed that the families Nucleatidae, Pygopidae and Discoliidae deserve to be singled out in a superfamily of their own. From palaeoecological/palaeogeographical considerations it is concluded that: (1) the greatest horizontal and vertical ranges were attained by more generalized stocks close to the stem group; (2) the above-mentioned "anomalous" occurrences represent yet another example of successive "waves" of Tethyan taxa that have spread to Australasian localities in different moments of the Jurassic; (3) this was probably achieved by "sea-mount hopping" in coincidence with transgressive events worldwide and rising peaks of global sea-level curves; and (4) the present position of New Zealand and the Sula Islands relative to the suturing line of the Tethys closure, and the nature of these faunal links, may be a reflection of both territories having been located on the same margin of Gondwanaland during Jurassic times.

Introduction

One of the favourite—and recurrent—topics in Prof. D.V. Ager's prolific production has been that of *Pygope* and its allies (numerous papers over the last three decades, see below). Thus, it seems most appropriate to put forward this reappraisal of the subject in a Special Issue dedicated to him.

Long ago he duly emphasised that stocks with a sulcate anterior commissure (i.e., "inverted" relative to the "normal" type of folding) or with a broadly expanded front (i.e., so-called "axiniform", or else deeply bilobed up to centrally perforated) showed a distinctive spatial distribution along the Alpine chains, excluding the Pyrenees (Ager, 1960, pp. 20–23, 1967, pp. 137–139, 144–148). Such pattern was alternatively termed "Alpine" or "Mediterranean" (within the Tethys) and was considered as one of the inner of a series of roughly concentric belts initially worked out in detail for the Early Jurassic, yet persistently recognizable for most of the Mesozoic (Ager, 1960, 1963, 1967, 1971, 1973, 1975, 1986b; cf. also Geyssant, 1966; Vogel, 1966; Middlemiss, 1973; 1984; Ager and Sun, 1988).

Though sometimes interpreted in terms of provinciality, Ager made clear that he believed that ecological rather than merely geographical control

---

Correspondence to: M.O. Manceñido, Division Paleozoologia Invertebrados, Museo de Ciencias Naturales, Paseo del Bosque, 1900 La Plata, Argentina.

0031-0182/93/$06.00

was involved, as he regarded these forms as characteristically adapted for living on calmer and deeper sea floors (Ager, 1963, 1965, 1968, 1971, 1976). Their sporadic occurrence as far north as Greenland in the Early Cretaceous was envisaged as the influence of a proto-Gulf Stream developed with the opening up of the Atlantic (Ager, 1971, 1973, 1975, 1986b; Owen, 1976; Ager and Walley, 1977; Sandy, 1991). More recently, many of these ideas have been further elaborated in successive papers by Vörös (1975, 1977, 1980, 1984a,b, 1986, 1987; Vörös et al., 1988) who postulates the former existence of a "Mediterranean microcontinent" independent from both the European and African shelves and itself differentiated into two subprovinces ("Carpatho-Sicilian" and "Apennino-Transdanubian"). An "Adriatic Microplate" inhabited by these faunas was likewise recognized by Ager (1980, 1986b).

With regard to palaeoecology, concurrent inferences have been derived from: (a) convergent development in unrelated brachiopod stocks, including not only fossil but also known deep-sea extant taxa (Ager, 1960, pp. 23–24, 1963, p. 49); (b) occurrence in facial settings dominated by calcareous mudstones and marls, with an associated fauna of ammonites (often phylloceratids and lytoceratids, sometimes just aptychi), belemnites, inoceramids, calpionellids, radiolarians and pelagic foraminifers (Ager, 1963, p. 210, 1965, p. 161; Vogel, 1966, pp. 430–434); and (c) functional morphological approaches to adaptive traits for optimizing oxygen absorption areas (Ager, 1960, p. 24, 1963, pp. 133–134) as well as most effective spatial separation of incurrent food-bearing streams from excurrent waste-carrying water jet(s), away from a muddy substrate (Ager, 1960, p. 24; Vogel, 1966, pp. 426–430, 435–437; Rudwick, 1970, p. 125, fig. 73). Confirmatory hydrodynamic flume experiments with a model placed across a current have been incidentally reported in dealing with Palaeozoic dicoelosiid analogues (Brower and Veinus, 1978, p. 1051). These evidences are all consistent with biotopes in which benthos-poor, extremely fine grained bottoms are combined with very quiet waters, involving high risk of recirculating a filtered stream plus an intrinsic deficiency in suspended food particles supply (and maybe in oxygen concentration too). Such environmental conditions may be found in bathyal to abyssal depths of the ocean (Steinmann, 1925; Ager, 1965; Vogel, 1966), or on (and around) sea mounts standing up from the ocean floor (Vörös, 1973, 1975, 1986; Ager, 1986b, 1991; Ager and Sun, 1988). It has even been suggested that small-sized adults of *Nucleata nucleata* may have been adapted to live in epibathyal conditions, perhaps attached as epibionts upon certain ammonites and thus benefitting from passive transport (Tchoumatchenco, 1986, p. 394).

From an evolutionary viewpoint, Buckman's highly speculative scheme (1906, plate 41) displaying no less than three vertical "genetic series" (equated to genera) and four horizontal "developmental stages", with fossils arranged in a matrix-like theoretical framework (showing few "empty boxes" indeed) was never accepted by Ager, on the grounds of Buckman's insufficient field information and disregard of actual stratigraphical succession. He was not convinced either by the phylogenetic ideas epitomized in a more conventional, rather "bushy", branching diagram by Jarre (1962, pp. 105–114, fig. 12). In Ager's opinion, the evolution of the group seems a classical example of a stock confined to a restricted environment, which repeatedly diversified in the same general area in Late Jurassic times and after the difficult episode of the Jurassic–Cretaceous boundary. Such radiation budded off from a main trunk of *Nucleata*-type sulcate forms with Triassic–Early Jurassic roots which, save for a mid-Jurassic near eclipse, continued unabated into the Cretaceous, at least until the Albian (Ager, 1965, p. 163, 1975, p. 155). This is aptly depicted in his latest tree, branched in a "candelabrum" fashion to reflect long periods of stasis and short evolutionary bursts (Ager, 1986a, fig. 2).

As a by-product of his studies, Ager also analysed possible biostratigraphical significance of representatives of the group, first in relation to the Jurassic–Cretaceous boundary (1975), and then providing an overall succession of dominant conspicuous species for the Jurassic of Tethyan areas (Ager, 1979, table 7).

On the other hand, since the *Treatise* (Muir-Wood, 1965), main contributions to family-level classification have been by Dieni et al. (1975), Dieni and Middlemiss (1981) and Cooper (1983).

According to this state of knowledge, neither Nucleatids nor Pygopids had ever been illustrated from circum-Pacific areas. The only incidental mention traced so far, corresponds to the preliminary identification of a terebratuloid from the Upper Triassic Torlesse terrane of Palmerston North, New Zealand, due to Ager (1986b, p. 388), "which may be *Nucleata* or a long-looped homoeomorph thereof" and whose presumed short-looped affinities have apparently not been elucidated yet. Genuinely, then, this contribution reports and documents the discovery of Jurassic Nucleatids in different islands of the Australasian region. In view of the undeniable palaeobiogeographical interest of these findings, also broader aspects of the distribution and relationships of the group are summarily reviewed and blended with unpublished results from the present author's thesis (Manceñido, 1978).

Systematic palaeontology

A new species from the Early Jurassic of New Zealand

In April 1990, systematic surveying of the Mesozoic fossils housed at the Department of Geology, University of Auckland [= AU], revealed the present material, still unidentified since being collected in 1971 by Prof. Grant-Mackie and others, from Murihiku terrane inland exposures in the Port Waikato area (North Island of New Zealand). Although no other fossil has been recorded from precisely the same stratigraphic interval, the bearing beds were assigned to the upper Ururoan on the basis of its normal occurrence about 90 m upstream from those yielding the diagnostic lower Ururoan bivalve *Pseudaucella marshalli* Marwick (J. Grant-Mackie, pers. commun., 1990–1991). Consequently, this suggests in standard terms a probable Toarcian (late Pliensbachian?–Aalenian?) age for the topmost Pongawhakatiki Siltstone.

Linguithyris agerorum sp. nov. (Fig. 1a–e)

Diagnosis: Medium-sized *Linguithyris* (about 30 mm wide, 25 mm long and 15 mm thick); with a heptagonal outline in top view, widest and thickest at front; with a broad, shallow, flattish, dorsal sulcus (about 22 mm in maximum width); anteriorly truncated to tenuously bilobed, with straight lateral commissure and gently arched linguiform extension at right angles to it; with an incurved beak (almost concealing delthyrial region), bearing a rather large, permesothyrid foramen.

Etymology: The species is named after Derek and Renée Ager.

Holotype: An almost complete steinkern with a corner damaged (No. AU 907). *Type locality*: Opuatia Stream, ca. 4 km downstream from Ponganui Road (Fossil loc. R13/f7048, grid ref. R13/732 247), New Zealand. *Comparisons*: The new species is first compared with the type species of the genus *L. bifida* (Rothpletz) (1886, p. 114, plate 5, figs. 17–19, 21, 23, 25–27) from the Bajocian of the Alps, which can be also wider than long; yet it bears a deeper, obtrapeziform linguiform extension and attains maximum width and thickness at mid-length. *L. nepos* (Parona and Canavari) (1882, p. 342, plate 10, figs. 1–4; Rothpletz, 1886, p. 416, plate 5, figs. 20, 22, 24; Jarre, 1962, p. 100, plate J, fig. 2; Ferrari and Manara, 1972, p. 315, plate 30, figs. 1, 2), from the Aalenian of northern Italy–Austria, is much smaller, with a "U-shaped" median sinus deflected back. *L. umbonata* (Buckman) (1918, p. 234, plate 20, fig. 4a; Muir-Wood, 1965, p. H802, fig. 679/4a–c), from the Bajocian of Dorset (England) and elsewhere, is narrower still, with a gibbous dorsal umbo and an early starting dorsal sulcus, parabolic in anterior view. *L. maximus* Tkhorzhevskij (1989, p. 26, plate 2, fig. 1a–v), from the early Bajocian of the Pieniny Carpathians, also tends to be longer than wide, more rounded and with a deeper central dorsal sulcus.

L. aspasia (Meneghini) is a Liassic species widespread from Turkey, Greece, Hungary, Czechoslovakia, Austria, Switzerland, across Italy to Sicily, Algeria, Morocco, Spain, which likewise shows a predominantly transverse shape, though bilobation is usually more neatly developed, with well-rounded lobes separated by a much retracted median deflection expressed in a well-detached ventral fold (cf. Zittel, 1869, p. 126, plate 14, figs. 1–4; G. Geyer, 1889, p. 14, plate 2, figs. 14, 15; Fucini, 1896, p. 213, plate 24, fig. 1; Buckman,

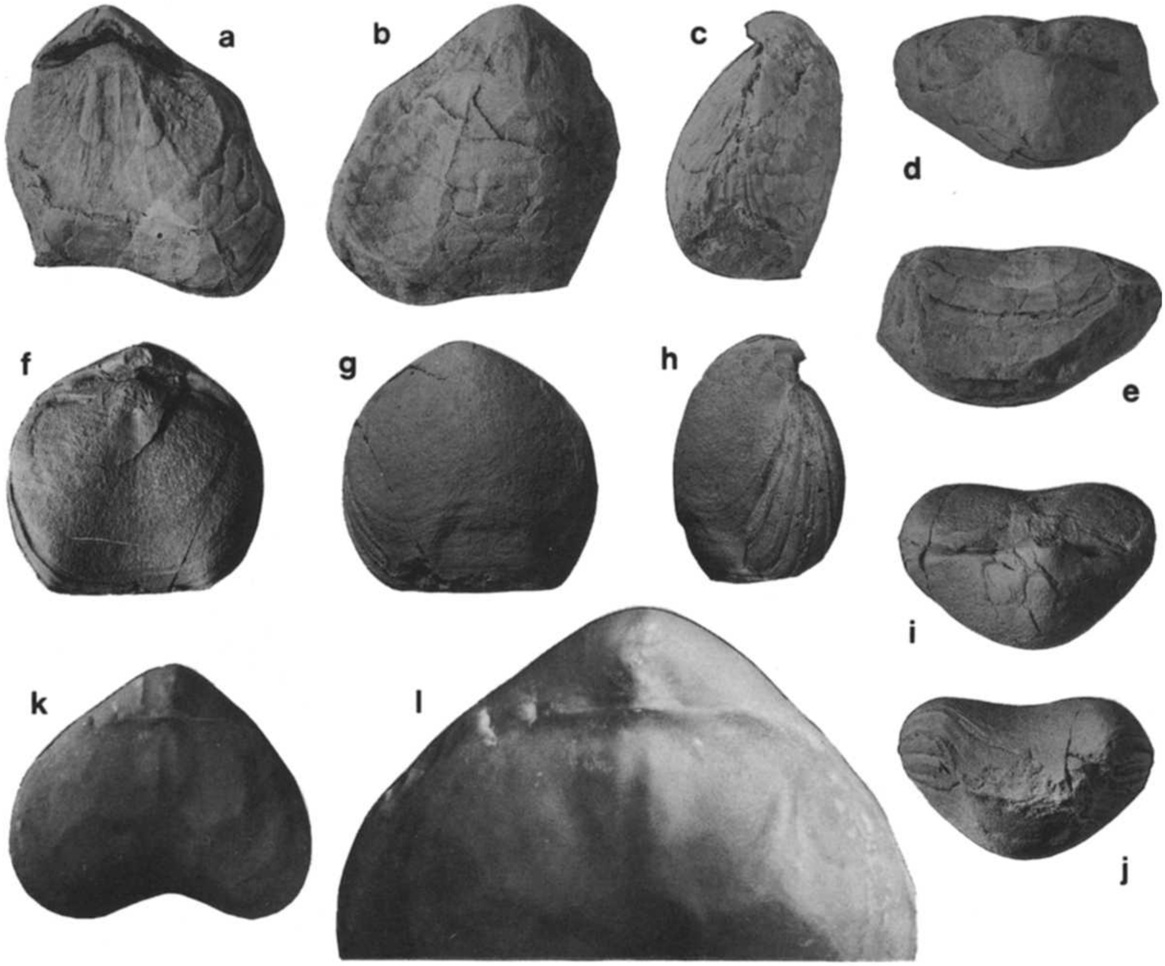

Fig. 1 (a–j) Specimens coated with ammonium chloride, whereas (k–l) are photographed under water to enhance features perceivable through translucent shell. (a–e) *Linguithyris agerorum* n. sp., AU 907 X 1.5, upper Lias, Opuatia Stream, North Island, New Zealand. (a) Dorsal view. (b) Ventral view. (c) Lateral view. (d) Posterior view. (e) Anterior view. (f–j) *Nucleata* ex gr. *bouei/ planulata* (Zeuschner), MLP 24892 × 1.5, upper Jurassic, the Sula Islands, Indonesia. (f) Dorsal view. (g) Ventral view. (h) Lateral view. (i) Posterior view. (j) Anterior view. (k–l) *Phymatothyris rheumatica* (Canavari), NMB L9542, middle Lias, Scavoviglia, Corfu Island, Greece. (k) Dorsal view (× 2). (l) Enlarged detail of (k) (× 4).

1906, p. 438, plate 41, fig. 23; Flamand, 1911, p. 872, plate 3, fig. 7; Dareste de la Chavanne, 1920, p. 39, plate 3, figs. 9, 10; Jimenez de Cisneros, 1923, p. 20, plate 3, fig. 4; De Gregorio, 1930, p. 33, plate 6, figs. 3, 27, 42, plate 7, figs. 9, 10; Renz, 1932, p. 28, plate 2, figs. 3, 5; Vigh, 1943, p. 331, plate 25, figs. 20–28; Jarre, 1962, p. 85, plate J, fig. 1; Siblík, 1964, p. 163, plate 7, fig. 3; Sacchi-Vialli and Cantaluppi, 1967, p. 100, plate 14, figs. 13–15; Brambilla, 1971, p. 470, plate 1, fig. 1; etc.). Less similar is *L. hughenini* (Rollier), from the Toarcian of Crussol, France (Dumortier, 1874, p. 216, plate 46, figs. 16–18), being slightly longer than wide and incipiently intraplicate.

In fact the overall shape of *L. agerorum* n. sp. is closely reminiscent of *Terebratula* (*Waldheimia*) *bilobata* from the Lias of Italy, which differs in its sharper and longer beak ridges and in being thickest at mid-length. Yet if the latter is long-looped (as implied by Zittel, 1869, p. 127, plate 15, figs. 1 2) such resemblance would be purely homoeomorphic.

A new record from the Late Jurassic of the Sula Islands

A couple of years ago, the writer recognized a well-preserved specimen in a sample kept unprocessed with collections from the Sula Islands obtained in 1976 by Westermann, Sato and Skwarko (1978). In spite of imprecisions surrounding accurate provenance, it is—not surprisingly—physically associated to inoceramids thus warranting brief description and illustration (Fig. 1f–j). According to S. Damborenea (pers. commun., 1989) the bivalve shells belong to the *Retroceramus galoi-haasti* lineage, which is well known in Heterian and Ohauan strata (of the New Zealand scheme) from the Southern Hemisphere. Hence, the age of the accompanying brachiopod may be approximately bracketed between Callovian and early Tithonian of the international scale (cf. also Westermann et al., 1978, table 1; Damborenea, 1990, fig. 4).

Nucleata ex gr. *bouei/planulata* (Zeuschner) (Fig. 1f–j)

Description: This is a medium-sized *Nucleata* (22.5 mm wide, 22 mm long and 14 mm thick), with an almost subcircular (anteriorly truncate) outline and a markedly ventribiconvex profile; with a flattened dorsal valve, and a rapidly widening median sulcus (up to 15 mm wide at front); with an erect to somewhat incurved beak pierced by a round, mesothyrid foramen (and not concealing delthyrial region): sulcate anterior commissure with a squarish linguiform extension perpendicular to straight lateral commissures; shell substance finely and densely punctate. *Material*: A complete steinkern with remains of partly decorticated shell (MLP 24892). *Comparisons*: The type species, *N. nucleata* (Schlotheim) from the Oxfordian and Kimmeridgian of southern Europe and northern Africa is considerably smaller in average size, has a more massive and prominent umbo, is more subpentagonal in outline and gibbous in profile, as revealed by comparison with the literature (Quenstedt, 1856–1857, p. 638, plate 79, figs. 14–16, 1868–1871, p. 360, plate 47, fig. 108 etc.; Choffat, 1947, p. 29, plate 16, fig. 9; Jarre, 1962, p. 87, plate J, figs. 6, 8; Muir-Wood, 1965, p. H802, fig. 679/1a–d; Malinowska, 1967, p. 86, plate 11, figs. 1–4; Barczyk, 1972, p. 155, plate 1, fig. 3; Renz et al., 1975, p. 445, plate 1, figs. 15, 16; Laurin, 1979, p. 418, figs. 1, 2; Cooper, 1983, p. 123, plate 36, figs. 7–9; etc.), and with own collections from the White Jura of the Swabian Alb. The present material does resemble, however, certain larger forms from the Oxfordian–Tithonian of France and Germany either interpreted by Jarre (1962, p. 90, plate J, fig. 7) as a depressed variant of *N. nucleata* and also compared to *N. aliena* (Oppel), or called *N.* cf. *nucleata* by Quenstedt (1868–1871, p. 361, plate 47, fig. 113).

As noticed by Dieni and Middlemiss (1981), it is sometimes difficult to discriminate within the plexus of Oxfordian–Berriasian forms referred to Zeuschner's nominal species *N. bouei* and *N. planulata* and may even correspond to a single highly variable taxon, spread from northern Morocco and southern Spain, along southern Europe, up to Crimea and the Caucasus. Typical *N. bouei*, however, are more cordiform and have a parabolic to almost "V"-shaped sulcus (cf. Zittel, 1870, p. 252, plate 13, figs. 15–24; Favre, 1875, p. 53, plate 7, figs. 13–15; Ksiażkiewicz, 1956, pp. 218, 355, plate 26, fig. 5; Jarre, 1962, p. 93, plate J, fig. 10; Geyssant, 1966, p. 75, plate 1, figs. 1, 2; Barczyk, 1972, p. 153, plate 1, figs. 1, 2; Lillo Beviá, 1977, p. 83, plate 3, figs. 3–5). Yet the similar W/L ratio and "open U"-like sinus, shown by some examples assigned by Favre (1877, plate 9, figs. 10–12), Geyssant (1966, plate 1, figs. 3–4) and Lillo Beviá (1977, plate 3, figs. 1–2) are comparable with those conditions in the Australasian specimen. Since it also approaches *N. planulata* (Zittel. 1870, p. 253, plate 38, figs. 3–5; Moiseev, 1934, p. 197, plate 17, figs. 12–15; Barczyk, 1972, p. 156, plate 1, figs. 4, 5; Sequeiros, 1977, p. 9, figs. 3, 4; Dieni and Middlemiss, 1981, p. 45, plate 4, fig. 4) and agrees very well with Moiseev's Tithonian material from the Caucasus, open nomenclature is advisable.

Also linked to the same group are the Oxfordian–Berriasian *N. rupicola* Zittel (1870, p. 252, plate 38, figs. 1, 2; Buckman, 1906, p. 445, plate 41, fig. 1; Jarre, 1962, p. 101, plate J, fig. 5; Geyssant, 1966, p. 76, plate 1, fig. 5; Barczyk, 1972, p. 157, plate 1, figs. 6, 7; Sequeiros, 1977, p. 9, fig. 3/2–3) and the Oxfordian *N. favrei* Rollier (1918, p. 261; cf. also Favre, 1876, plate 7, fig. 5; Jarre, 1962, plate J, fig. 4), but they are much more transversely expanded and bilobed. Actually, Tkhorzhevskij (1989) introduced a genus *Vjalovithyris* on the basis of Transcarpathian materials attributed to Zittel's *V. rupicola* and to a new species *V. pinguis* from Tithonian and Berriasian deposits respectively. (He included Zeuschner's *V. bouei* and Geyssant's *V. rifensis*—elevated to species rank—as well). His only figured specimen is rather plump and mot markedly bilobed, thus so similar as to be regarded congeneric with the Indonesian shell. Yet, in view of the relative foramen size in the latter and of missing data about muscle scars in both, assignment to *Nucleata* s.l. provides a fairer statement of affinities until other important features of all these forms become better known. This does not preclude that in the future perhaps they could be referable to *Vjalovithyris*. However, nominal genera such as this (or like *Kubanithyris* Tkhorzhevskij 1989), which appear to be based on minor differences of degree rather than of kind, doubtfully deserve subgeneric status at the very most.

Taxonomic position of certain Liassic nucleatids from Europe

Considerable debate has surrounded the proper generic allocation of many Early Jurassic nucleatids, such as Meneghini's "*Terebratula aspasia*", the commonest of them all. Contemporaneous authors have alternatively referred this and related species to *Propygope* (Ager, 1959, 1975; Siblik, 1964; Ager and Walley, 1977; Elmi and Alméras, 1984; Tchoumatchenco, 1986), to *Glossothyris* (Jarre, 1962; Ager, 1965), to *Nucleata* (Sacchi-Vialli and Cantaluppi, 1967; O.F. Geyer, 1967; Brambilla, 1971) and, more recently, to *Linguithyris* (Vörös, 1984a,b, 1986, 1987, 1990; Dulai, 1990). According to *Treatise* descriptions (Muir-Wood, 1965), *Propygope* Bittner differs in possessing a strong dorsal median septum (though serial sections of the Triassic type-species were not produced), as opposed to the short, ridge-like (almost negligible) myophragm of pygopids and nucleatids. *Glossothyris* Douvillé is a junior objective synonym of *Nucleata* Quenstedt, which in turn is not readily distinguishable from *Linguithyris* Buckman, except for details of the dorsal adductor muscle scars (short and divergent in the latter instead of curved and converging anteriorly in the former) and other subtleties not always properly recorded in the literature. Admittedly, some Italian authors even suspect that subjective synonymy might be involved. Conversely, Vörös, a leading authority in Mediterranean brachiopod faunas, has consistently adopted *Linguithyris* for Liassic and early Dogger species and *Nucleata* only for younger ones. Pending proper investigation of adductor scars of many species, it seems premature to dismiss the possibility of (at least partial) coexistence between *Linguithyris* and *Nucleata*. Where known, illustration of muscle patterns, as in *L. nimbata* by G. Geyer (1889, plate 2, fig. 13) or *L. agerorum* (Fig. 1a), would lend support to this criterion, which is thus provisionally followed for the purposes of this paper.

In more general terms, the Appendix contains a concise synopsis of the personal ideas (partly stated above or to be exposed below) about updated scope and hierarchy in classification.

In this connection, it is also important to reasses the relationships of the Liassic genus *Phymatothyris* Cooper and Muir-Wood, an avowed substitute for *Pallasiella*, which was initially proposed by Renz (1932) as a subgenus of the catch-all genus *Terebratula* but proved to be preoccupied. Moreover, the taxon has unfortunately remained poorly understood ever since, as reflected by its placement in the *Treatise* (Muir-Wood, 1965, pp. H813, H814) in an uncertain subfamily of the Cancellothyrididae. This misconception has presumably been influenced by the indecisive original treatment by Renz (1932, pp. 40, 41) who made comparisons even with athyrides and pentamerides. Though further on (op. cit., p. 42) he duly realized that this was just a matter of convergence in external appearance, the issue was confused enough to obscure any evidence of strong links with the Nucleatidae, as favoured by the present author (1978 and herein). The illustration of upside-down anterior views certainly did not help reviewers with the unravelling process.

Diagnostic features pointed out by Renz (1932;

and repeated by Muir-Wood, 1965) are swollen, very much incurved umbones (concealing foramen), associated with thickening of the valves in these areas. Except for that, most external characters, such as a finely (endo)punctate shell, unornamented but for growth lines, as well as the neatly sulcate frontal commissure of most species (including the type), suggests proximity to contemporaneous *Nucleata*-like stocks. Furthermore, Renz's description of adductor muscle scars as "länglichen" (=elongated) was extremely uninformative, and the writer was able to observe conspicuous "horseshoe-shaped" dorsal scars in the Greek material of *Phymatothyris rheumatica* (see Fig. 1k l same, as Renz 1932, plate 3, fig. 8). This key feature had been properly illustrated for the Upper Jurassic *Nucleata nucleata* (Schloth.) by Buckman (1918, plate 20, fig. 2ax, refigured by Muir-Wood, 1965, fig. 679/1d). It is also unmistakably shown (though not described) by Dieni et al. (1975, plate 34, figs. 4 6) on internal moulds of one of the youngest species of the genus, the uppermost Albian *N. mediterranea* Dieni and Middlemiss. The present author further recognized it in Prof. Ager's own collection of various members of the genera *Nucleata* and *Pygope* from the Upper Jurassic to the Lower Cretaceous of several European countries. So in spite of having escaped the attention of previous authors (e.g. Muir-Wood, 1965; Cooper, 1983; etc.) for characterization at family level, it appears to be widespread throughout nucleatids and pygopids (both in terms of age and taxa where it is present). It seems to occur even among Cenozoic representatives of the Discoliidae. Whilst the author is not at all a zealous believer in Buckman's doctrine of muscle scars as ultimate arbiters in brachiopod classification (which has fallen in discredit, cf. Ager, 1990, pp. 15 17), this particular case may be worthy of more attention. Obviously, such exceptional scar patterns are not found in other terebratulides (except perhaps in some forms classed as Nucleatulinae), and certainly neither in athyrides nor in pentamerides.

Thus the logical conclusion that *Phymatothyris* belongs to the Nucleatinae appears justified. In addition, the specimen figured herein (Fig. 1k) also reveals widely divergent dichotomous vascular markings (better displayed than in Canavari, 1883, plate 10, fig. 5), which may be further relevant to this issue.

Regarding the potential adaptive value of an extremely reduced or totally obliterated foramen, it is now known that in living members of the terebratellid genus *Neothyris* a free-lying mode of life on muddy bottoms is achieved with concomitant closure of a tiny pedicle opening by a chitinous plug (and apical "counter-weight" thickening) as described by Richardson (1981) and personally observed in aquaria at Portobello Marine Station (on ocassion of the 2nd. Int. Brachiopod Congress, 1990). The remarkable aspect of the early Jurassic ecological counterpart under consideration, would be that, judging from longitudinally sectioned specimens of *P. kerkyraea*, shell material was apparently involved in the plugging process in *Phymatothyris*.

Distribution in space and time

The palaeogeographical distribution is presented in four palaeocontinental reassembly maps (adapted from Smith and Briden, 1977, with palaeopositions of Turkey and Madagascar-Greater India after Scotese, 1991) corresponding to 180, 160, 140 and 120 Ma ago, respectively, i.e., Early Jurassic to Early Cretaceous times (Figs. 2-5). A synthetical account of occurrences plotted on each map, following a regional arrangement, is given immediately below.

The Early Jurassic

Many nominal species are involved, and even if their precise generic allocation may need further study (as commented in the preceding section), the overall picture would not be substantially altered (Fig. 2). For more detail in the Mediterranean areas see also Vörös (1984b, 1987, 1990).

Species now referable to *Linguithyris* and *Securithyris* have been reported from Murcia and Alicante provinces, southern Spain (Jimenez de Cisneros, 1923, 1935; O.F. Geyer, 1967) where they are part of the mid-Liassic "Pygope Aspasia" fauna, but are unknown from the Iberian ranges and the Pyrenees, as well as from central France and Britain. Simple sulcate *Linguithyris* occasion-

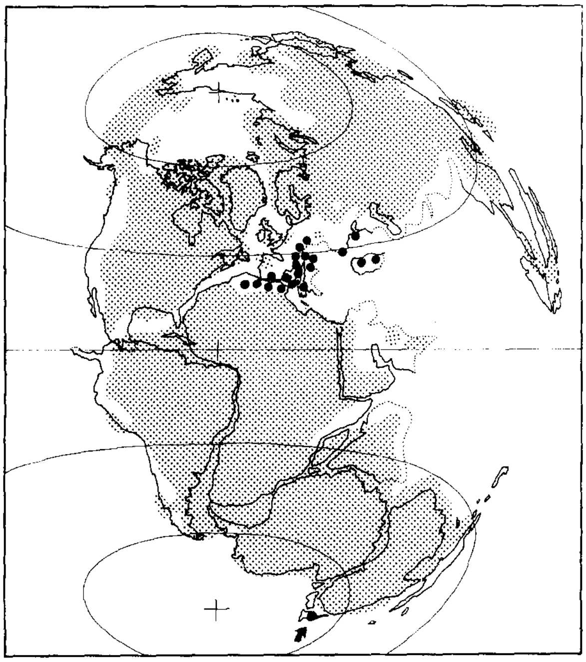

Fig. 2. Early Jurassic occurrences of *Linguithyris*, *Phymatothyris* and *Securithyris*, see discussion in text (arrow points to new record).

ally occur in Crussol, southern France (Dumortier, 1874) and in Wurttemberg, southern Germany (Rau, 1905). They become more common, and are sometimes accompanied by *Securithyris*, in Switzerland (Parona, 1885; Renz, 1932; Wiedenmayer, 1963; Brambilla, 1971), in northern Italy, from Piemonte to South Tyrol (Uhlig, 1879; Parona, 1892; Dal Piaz, 1907; Sacchi-Vialli and Cantaluppi, 1967; Brambilla, 1971), in the Northern Calcareous Alps of Austria (Oppel, 1861; Rothpletz, 1886; G. Geyer, 1889; Böse, 1893, 1897), up to eastern Czechoslovakia (Siblík, 1964, 1967).

In central Italy (the Apennine ranges, from Tuscania to Umbria) species of *Phymatothyris* may be added (Zittel, 1869; Canavari, 1880, 1881, 1882, 1883; Parona, 1883; Principi, 1910). Similar occurrences extend to Calabria (Taddei-Ruggiero and Vörös, 1987) and Sicily (Gemmellaro, 1874; Fucini, 1920; De Gregorio, 1930), both southern Italy; to Bakony Forest–Gerecse, in Hungary (Vigh, 1943; Vörös, 1980, 1984a,b, 1986, 1987); and to Corfu–Epirus, in western Greece (Renz, 1932; Manceñido, 1978).

In Liassic deposits of northern Africa, *L. aspasia* is further known from Tunisia (Ager colln., unpubl.), from Algeria—Oranie, Tiaret and Guelma areas—(Flamand, 1911; Dareste de la Chavanne, 1920; Elmi and Alméras, 1984; Tchoumatchenco, 1986) and from the eastern High Atlas of Morocco (Dubar, 1962, who also mentioned *S. adnethensis* from there).

Presence of *Linguithyris* in northern Turkey (Yacaçik and Bayburt) was substantiated by Ager (1959, as "*Propygope*"), whereas a presumable *Securithyris* from the first Turkish locality requires confirmation. Moiseev (1934, 1947) identified a Liassic species from Crimea which may be a *Linguithyris*, or a *Nucleata* according to Tchoumatchenco (1990), who subsequently retrieved it (as *N. bodrakensis*) from exotic deposits in eastern Stara Planina, Bulgaria.

To those, *L. agerorum* n. sp. from the western coast of New Zealand North Island, is added herein and therefore represents an important new record for the Lower Jurassic at global scale.

The Middle Jurassic

Records shown in Fig. 3 refer either to *Linguithyris* or *Nucleata* (and include *Kubanithyris*, cf. above discussion in the previous section). For more detail in the Alpine areas see also Vörös (1984b, 1990).

The type species of *Linguithyris* and several "satellite" nominal species have been recognized over southern Europe. In the Iberian peninsula, Portuguese records comprise those from the Bajocian (Alpine facies) of Cesareda, the lower Dogger of Guilhim and the Callovian of Cape Mondego and Algarve (Choffat, 1880, 1947; Mouterde et al., 1979). Similarly, there are mentions for the upper Bajocian–lower Bathonian of the Cantabrian area, northern Spain (Dubar, 1931) and for the Middle Jurassic of the Murcia province, southern Spain (O.F. Geyer, 1967).

The genus even reached southern Britain, occurring in Bajocian beds of Dorset (Buckman, 1918; Muir-Wood, 1965), in addition to France, the middle–upper Dogger of Ardeche, Voulte and Crussol (Rollier, 1918; Jarre 1962), to Switzerland, the middle–upper Bathonian of the Friburg Alps (Horwitz, 1939), to Austria, the Dogger of the Glarnish

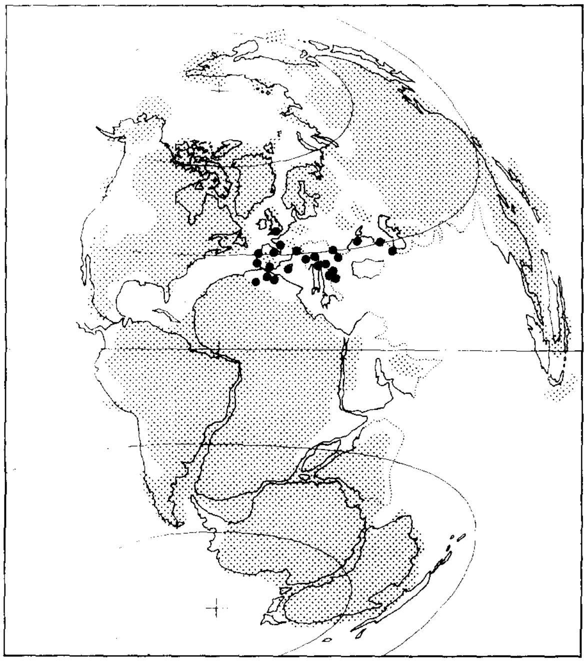

Fig. 3. Middle Jurassic occurrences of *Linguithyris* and *Nucleata*, see discussion in text.

and the Klaus and Vils Alps (Rothpletz, 1886; Rollier, 1918; Böse and Finkelstein, 1892); to Italy, the lower – upper Dogger of Trentino, Garda Lake and Sette Comuni (Parona and Canavari, 1882; Jarre, 1962; Ferrari and Manara, 1972, etc.); to Czechoslovakia, the middle–upper Dogger of the Pieniny Klippen belt (Siblik, 1966), to Ukrania, the lower Bajocian–lower Bathonian of the Pieninian Carpathians (Tkhorzhevskij, 1989) and to Hungary, the Bajocian of the Bakony Forest (Vörös, 1984b). It extended westwards along northern Africa to Morocco–Algeria—the Aalenian or upper Toarcian of the eastern High Atlas (Dubar, 1950), the Bathonian of the Oudjda region (Dareste de la Chavanne, 1930) and the Rhar Roubane horst (Elmi and Alméras, 1984)—and as far east as to Russian Transcaucasia, the lower Bajocian of Negram (Prozorovskaya, 1985). Besides, a similar nucleatid (*Kubanithyris parvus* Tkhorzhevskij 1989) has been described from the upper Bajocian of the northern Caucasus.

Species of *Nucleata* have been recorded from the Callovian of Ardeche and Vendee in France (De Grossouvre, 1891; Rollier, 1918; Jarre, 1962), the Callovian of the Pieniny Mountains in Poland (Uhlig, 1881), the upper Bajocian/lower Callovian of the Yugoslavian Carpatho-Balkanids (Tkhorzhevskij and Radulovicj, 1984), the Bathonian–Callovian of the Ukranian Carpathians (Tkhorzhevskij and Radulovicj, 1984; Tkhorzhevskij, 1989), the upper Callovian of the Bulgarian Prebalkans (Tchoumatchenco, 1978), and the middle–upper Callovian of Crimea (Kamyshan and Babanova, 1973; Tkhorzhevskij, 1989).

The Late Jurassic

Combined plottings of *Nucleata* (includes *Vjalovithyris*) and *Triangope* are given in Fig. 4. For more detail in the Mediterranean areas see also Geyssant (1966) and Vörös et al. (1988).

The type species of *Nucleata* and a number of additional nominal species are found over a wider area in southern and eastern Europe. There are occurrences in the Oxfordian of Penha Longa, Albarraque and Albufeira, Portugal (Choffat, 1947; Marques and Rocha, 1981), as well as in the upper Oxfordian–Tithonian of the subbetic ranges, prov-

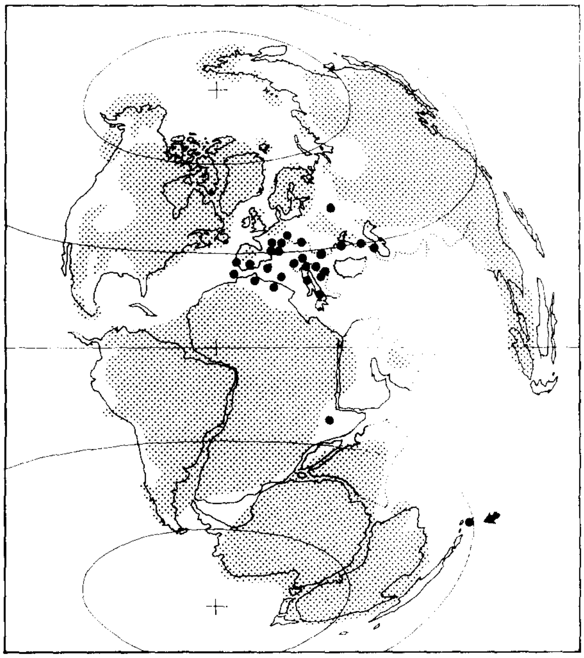

Fig. 4. Late Jurassic occurences of *Nucleata* and *Triangope*, see discussion in text (arrow points to new record).

inces of Cordoba, Sevilla and Alicante (O.F. Geyer. 1967; Sequeiros, 1977; Lillo Beviá, 1977) and the Tithonian of Majorca (Geyssant, 1966), in southern Spain. Additional findings are known in Oxfordian, Kimmeridgian and Tithonian deposits of France and Switzerland: from Ardeche (Rollier, 1918; Jarre, 1962; Geyssant, 1966), Causses (De Brun and Marcelin, 1934), Indre (Jarre, 1962), Provence (Rollier, 1918; Jarre, 1962), the Maritime Alps and Subalpine chains (Favre, 1875; Jarre, 1962; Geyssant, 1966; Laurin, 1979), the Argovian Jura (Quenstedt, 1868–71; Boullier, 1981), and the western and central Alps (Favre, 1876, 1877, 1880; Rollier, 1918; Blanchet, 1929; Jarre, 1962). Likewise, in Oxfordian–Kimmeridgian beds of southern Germany and Austria, including well-known sites along the Swabian–Bavarian ranges (Quenstedt, 1856–1857, 1868–1871; Rollier, 1918; Muir-Wood, 1965; Cooper, 1983, etc.) and in the eastern Alps, near Viena (Rollier, 1918; Geyssant, 1966).

In Italy, several Kimmeridgian–Tithonian localities of the southern Alps (Nicolis and Parona, 1885; Dieni and Middlemiss, 1981), of the Central Apennines (Zittel, 1869, 1870) and of Sicily (Gemmellaro, 1876) have yielded *Nucleata* (cf. also Geyssant, 1966). It is also known along Tithonian exposures of the Pieniny Klippen Belt, including classical places like Puchow and Stramberk in Czechoslovakia (Quenstedt, 1868–1871; Zittel, 1870), Transcarpathia (Tkhorzhevskij, 1989) or Rogożnyk, Czorstyn and Biala Woda in Poland (Zittel, 1870, Barczyk, 1972) and further Polish occurences, as old as lower Oxfordian, from the Holy Cross Mountains (Malinowska, 1967; Barczyk, 1969), or from exotic blocks at Bachowice–Woznicki (Ksiażkiewicz, 1956; Vörös et al., 1988). This genus is further recorded from the Tithonian of the Transdanubian central range in Hungary (Geyssant, 1966; Vörös et al., 1988), the Oxfordian–Tithonian of the Prebalkans of Bulgaria (Tchoumatchenco, 1978), the Oxfordian of the Ryazan region, Russian platform (Makridin, 1964) and the Oxfordian–Tithonian of the Caucasus (Moiseev, 1934; Makridin, 1964) and Crimea (Retowski, 1894).

In Africa, various Late Jurassic *Nucleata* have been found, too: from upper Oxfordian–lower Kimmeridgian limestones dredged from the Atlantic continental slope (Mazagan escarpment) off northwestern Morocco (Renz et al., 1975); as well as from outcrops, such as the Tithonian of Moyen Ouerrha, northern Morocco (Geyssant, 1966), the Oxfordian–Kimmeridgian of the Tiaret area, Algeria (Tchoumatchenco, 1986), and even from the Malm of Harro-Rufa and Cabenaua, in the Ethiopian region (Dacqué, 1905; Basse, 1930).

A significant extension farther east corresponds to the new record from the Sula Islands herein preliminarily determined as *Nucleata* ex gr. *bouei/planulata*.

On the other hand, *Triangope* is known mainly from the Tithonian (and seldom Kimmeridgian) of southern Spain and the Balearic Islands, the Lombardian and Venetian Alps, the central Apennines and Sicily, the Pieniny Mountains, the Transdanubian central range, western Greece, northern Algeria and the Moroccan pre-Rif (Quenstedt, 1868–1871; Zittel, 1869, 1870; Vigh, 1943; Jarre, 1962; Geyssant, 1966; Geyssant and Mascle, 1970; Dieni and Middlemiss, 1981).

The Early Cretaceous

What has been said about the previous map also applies to Fig. 5 (which is appended for the sake of completeness). For more detail in the Mediterranean areas see also Geyssant (1966), Middlemiss (1973) and Vörös et al. (1988).

Under several specific names, the Cretaceous *Nucleata* have been reported from many European countries: the Lower Cretaceous of southern Spain, the Balearic Islands (Geyssant, 1966) to subbetic ranges (Middlemiss, 1973; Calzada, 1985); the Berriasian–Albian of southern France—Provence, Ardeche, Isere—(d'Orbigny, 1850; Jarre, 1962; Middlemiss, 1973); the Neocomian of the Swiss Alps (Jarre, 1962; Middlemiss, 1973); the lower Neocomian of the southern Alps (Geyssant, 1966; Dieni and Middlemiss, 1981) and the upper Albian of east-central Sardinia, Italy (Dieni et al., 1975); the Lower Cretaceous of northeast Moravia, Czechoslovakia (Nekvasilova, 1980); the Berriasian of the Pieniny Mountains, Poland (Barczyk, 1972); the Pieninian Carpathians, Ukrania (Tkhorzhevskij, 1989); the Lower Cretaceous of Bakony Forest, Hungary (Fülop, 1964); the Neo-

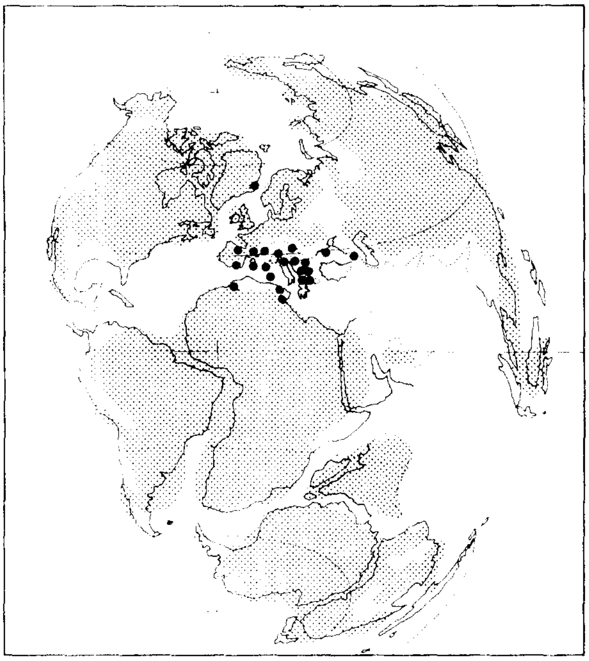

Fig. 5. Early Cretaceous occurrences of *Nucleata* and *Triangope*, see discussion in text.

comian from Brassov, Romania (Jekelius, 1915); the Lower Cretaceous of the Prebalkans near the Bulgarian Yugoslavian border (Middlemiss, 1973); and the Barremian of Crimea and the Aptian of the Caucasus (Smirnova, 1972).

North African records include: the Aptian Albian from the western High Atlas of Morocco (Ager, 1974); the upper Albian near Bone, Algeria (Dieni et al., 1975) and, the youngest *Nucleata* of all, from the Cenomanian of Kessera, central Tunisia (Peybernès and Calzada Badia, 1981), which already belongs to the Upper Cretaceous.

But perhaps equally or more interesting Lower Cretaceous occurrences are those from the Cantabrian area of northern Spain (Middlemiss, 1973) and from farther north up in the east coast of Greenland (Owen, 1976), which have been interpreted as linked with the opening of the Bay of Biscay and the North Atlantic (cf. Ager, 1971; Middlemiss, 1973; Ager and Walley, 1977; Sandy, 1991).

On the other hand, *Triangope* is represented in the Berriasian of the Balearic Islands, the Neocomian of the Subalpine chains, the lower Neocomian of the Lombardian, Venetian and eastern Alps, the Valanginian of northeast Yugoslavia, and the Berriasian Barremian of Hungary (Gočanin, 1938; Jarre, 1962; Fülop, 1964; Geyssant, 1966; Dieni and Middlemiss, 1981, and references therein).

Implications

As pointed out by Vörös et al. (1988, pp. 71 73), *Triangope* (and certain pygopines) were always restricted to the Apulian margin, whereas other, rather generalized, sulcate (or perforate) forms (including *Nucleata*), successfully invaded the northern margin of the Tethys in the Late Jurassic. Though all these forms have been traditionally regarded as deep-water, "Mediterranean", on the basis of their special morphology, it is possible that less specialized stocks (such as *Nucleata* itself) may have been relatively more eurytopic (cf. also Vogel, 1966, p. 434; Middlemiss, 1973, p. 117, 1984, p. 168), thus able to afford greater spatial and temporal ranges, than the most derived ones. In this context, the fact that a much specialized offshoot like *Phymatothyris* appears circumscribed to peri-Adriatic localities by the Early Jurassic already, ought not be surprising but expected.

Besides, the discovery of representatives of *Linguithyris* and *Nucleata* as far away from the Mediterranean as New Zealand and Indonesia strengthens the views of New Zealand colleagues (e.g. Fleming, 1967; Grant-Mackie, 1985; Stevens, 1990), who have rightly recognized a manifest influx of other Tethyan immigrants in the southwest Pacific, already by the late Lias (upper Ururoan) and very prominently in the Malm (Heterian Ohauan of the local scale).

Perhaps it is not without significance that such "anomalous" occurrences are roughly coincident with transgressive events that affected extensive areas all over the world (cf. Ager, 1981) and/or with well-known peaks of global eustatic curves (cf. Haq et al., 1987; Stevens, 1990). It is quite simple to envisage that the rising of the sea level towards global maxima, by a process analogous to "overspilling", would have "carried away" these benthonic organisms, presumably at larval stage, over increasingly longer oceanic stretches. The natural consequence could have been either a longterm propagation over new areas without abandonment of the original territory, i.e., prochoretic migration (sensu Termier and Termier, 1956), or a short-term invasion out of the original range via a transgressive episode, i.e. esbolic migration (sensu Termier and Termier, 1956). Though interpretation is admittedly difficult with the limited data at hand, perhaps the latter may be favoured since dispersal of this kind of sedentary marine animals with short-lived planktonic larvae is highly dependent on availability of appropriate bottom conditions suitable for settling, which may have served as "stepping stones". In the case of Mesozoic brachiopods, it could be the result of a mechanism that has been called "sea-mount hopping" (Ager, 1986b; Vörös, 1987; Vörös et al., 1988), which certainly implies a filtering action, fit to explain the infrequency of similar findings. Other interesting aspects of how the spatial ranges of circalittoral (or deeper water) biota may be influenced by peculiarities of life style were pointed by Masse (1992, pp. 332–338). Thus the possibility that occurrences at higher palaeolatitudes may correspond to shallower depths has to be kept in mind, when analysing past distributions of sciaphilous, relatively stenothermal and rather eurybathic organisms.

Such results can be also compared with the insightful analysis of biogeographical boundaries of the Wallacea region, based upon Jurassic marine bivalves, by Hayami (1984, 1987). With the proviso that "absence of evidence" is not necessarily equivalent to "evidence of absence", these new findings of nucleatids in New Zealand as well as in the Sula Islands, coupled with the lack of any records for the Jurassic of southeastern Asia (from Thailand, Viet-Nam, Borneo, the Philippines to Japan) are in agreement with Audley-Charles' (1981) line (being also compatible with Wallace's line), whilst being inconsistent with Weber's and Lydekker's lines (cf. Hayami, 1984, fig. 3, 1987, fig. 1). This may add a little supplementary support to the interpretation that both the Sula Islands and New Zealand belonged in the Jurassic to the margin of Gondwanaland (cf. Audley-Charles, 1981; Metcalfe, 1991), and thus are presently located on the same side of the suturing between Eurasian and Australian continental crust from opposite shores of the Tethys (however flexuous that line may nowadays be).

Overview of the evolutionary history

Bearing in mind the rather generalized dorsal muscle pattern of some Early Jurassic forms such as *Linguithyris* and *Securithyris*, it seems reasonable that the Nucleatidae in general, and the Nucleatinae in particular, probably represent—if not the stem group itself—at least a persistent lineage closely approaching the ancestral stock. Within this family, an early radiation apparently took place in Pliensbachian–Toarcian times. This is partly exemplified by the development of strong bilobation coupled with a receding dorsal median sinus (as in *L. aspasia*) or by the beak-like anterior protrusion of the linguiform extension (as in *L. chrysilla*) or by the increased gibbosity and loss of functional pedicle opening (as in *Phymatothyris*). Moreover, it is further manifested in the acquisition of the conspicuous securiform (or "axiniform" or "triangulate") shape so typical of the various species of *Securithyris* (sometimes deltoid rectimarginate, sometimes with concave sides, sometimeswith ligation and even with incipient broad sulcation) which thus deserve to be segregated as a new subfamily (Securithyridinae).

A much more conservative existence seems to have prevailed among the Nucleatinae throughout the Middle and well into the Upper Jurassic. In fact the only noticeable departure from the generalized simple sulcate forms (in which the horse-shoe dorsal muscle pattern appears well established) being recorded within the Aalenian–early Kimmeridgian interval, is the local modification of the "glossothyridoid" stage (Buckman, 1906) by intraplication of the anterior commissure (sometimes so gentle to scarcely affect the relief of the fold and sulcus). The taxonomic importance of this feature, however, has been given quite dissimilar weight by different authors, being variously interpreted as diagnostic for full-specific discrimination by some (Rollier, 1918; Tkhorzhevskij and Radulovicj, 1984; Tkhorzhevskij, 1989) or else merely regarded as intraspecific variation by others (Jarre, 1962; Malinowska, 1967; Barczyk, 1969; Laurin, 1979).

The lineage experienced another sudden diversification phase in late Kimmeridgian–early Tithonian times, with side effects discernible up to the

Barremian. This subsequent radiation near the Jurassic–Cretaceous boundary was more spectacular, giving rise to the well-known Pygopidae. They are here regarded as the former crown group, in which frontal widening was most notably achieved by deep bilobation ("bifidate" stage sensu Buckman, 1906), eventually attaining the most peculiar condition "with a keyhole in the middle" (i.e. "perforate" stage sensu Buckman, 1906), as well as radial plication within the fold/sulcus system; an unmistakable, very specialized morphological spectrum, characteristical of the Pygopinae in its strictest sense.

In addition, the unusual deltoid to securiform shapes (triangulate and quadrangulate imperforate stages sensu Buckman 1906) were developed once again by the various species of *Triangope*. Since there is strong consensus (Ager, 1975, 1986a; Dieni and Middlemiss, 1981; Vörös, 1983) that this was accomplished independently from the Early Jurassic event and without the fanciful phylogenetical "gradual closing up" of the central perforation by coalescence conceived by Buckman (1906) and reluctantly endorsed by Jarre (1962), here too, a new subfamily (Triangopinae) is required to accomodate this iteratively derived offshoot.

Both the mid-Liassic and end Jurassic radiations seem to have exploited an array of adaptive pathways leading to efficient separation of inhalant from exhalant currents, expansion of mantle marginal areas, most probably advantageous to cope with relatively weak-energy, suspended-nutrients-deficient (sometimes oxygen-poor) waters, as already pointed out by previous authors on the grounds of empirical observations, morpho-functional analyses, and/or taphonomical evidence (Ager, 1960, 1963, 1965, 1968; Vogel, 1966, 1986; Rudwick, 1970; Vörös, 1986). Regarding Vogel's contention, it should be recalled that oxygen poor does not necessarily mean reducing conditions as in euxinic bottoms. Brachiopods in general being regarded as "minimal organisms" (Thayer, 1981, pp. 117, 118) one could envisage natural selecting mechanisms acting upon certain lineages towards adaptation to combined effect of low oxygen levels and great depths, whereby increased hydrostatic ambient pressure may render respiration under very low oxygen concentrations feasible.

After that, only the mainstream "glossothyridoid" branch lingered on until the latest Albian (last records of members of the genus *Nucleata*, then known) and the classical version of the story likewise used to end at this point, their (virtual) extinction being blamed on adverse effects of widespread black, bituminous and sulphurous deposits, linked with the opening of the South Atlantic, towards the end of Early Cretaceous times (Ager, 1981, p. 162). It is now evident that the youngest species (*N. burolleti*) managed to reach the Late Cretaceous (Cemomanian) in central Tunisia (Peybernès and Calzada, 1981), at a time when the Discoliid *Moraviaturia diphimorpha* (Stol.) was present in southern India. From the Maastrichian of north- and southwest Turkmenistan, a new genus *Bolgarithyris* has been recognized by Titova (1986, 1992) who ascribed it to the Nucleatidae; alternatively, it could be interpreted either as the youngest Triangopinae or perhaps as an early Discoliinae already.

Anyway, with the fairly recent removal of *Trigonithyris* to its own family by Radulovic (1986), the Discoliidae would thus have a chronological span from the Late Cretaceous to Recent, its nominotypic subfamily being centred around *Discolia*, probably *Moraviaturia* and almost certainly *Waisiuthyrina*, too. To them, Cooper (1983) has added *Xenobrochus*, an extant genus attributed to the Discoliinae, as well as the newly erected subfamily Aenigmathyridinae containing half a dozen exclusively Cenozoic (Paleocene to Recent) genera.

It is of little relevance whether they have always inhabited deep waters (cf. Vogel, 1966) or both deep and shallow but very calm waters (cf. Ager, 1965; Ager and Walley, 1977) and only became confined to abyssal depths by the end of the Mesozoic era (objections to strict bathymetric control were raised by Vörös, 1975, 1986). The attractively persuading observation is that one may now start viewing the adaptive morphological developments achieved by these families as the reflection of a genetic link of some sort, rather than as the capricious result of deceptive homoeomorphy (cf. also Vörös, 1983). In such case, no matter that someone might find "pygopacean" or "nucleatacean" preferable on the grounds of euphony or tradition, by virtue of the Coordinate Categories and Priority nomenclatural principles, Discoliacea is the name to be adopted for a superfamily embracing them all. Perhaps this choice has an advantage anyway, for availability of an extant type genus renders it amenable to independent testing from other modern avenues of research (shell ultrastructure, biochemical/molecular analysis) in relation to other living taxa. Moreover, it might be tempting for someone to attempt tracing back an even more simplified evolutionary pattern, with a very early dichotomy, linking all deltoid-securiform subfamilies in one branch, whilst grouping the sulcate (plus perforate) subfamilies in another. Yet, because important gaps of key evidence still have to be filled in, it seemed advisable at this stage to adopt the more prudent approach discussed in this section and summarized in the Appendix.

Conclusions

(a) Among the Nucleatidae, a remarkable taxon of the Tethyan Mesozoic, conservative stocks close to the stem group appear to have attained the widest geographical distribution and longest chronological endurance. This may also apply to the Pygopidae, mutatis mutandi.

(b) Occurrence of representatives of this typical "Mediterranean" family as far east as New Zealand and the Sula Islands denote the influence of successive "waves" of Tethyan immigrants in the soutwest Pacific, at various times during the Jurassic, corroborating opinions expressed by previous authors on other grounds.

(c) The approximate coincidence of such occurrences with transgressive events that affected wide areas of the world and with well-known peaks of global eustatic curves may be in itself meaningful. Maxima of sea-level rising, may have favoured larval stages of these benthonic organisms to be carried farther away over the ocean, thus resulting in the detected esbolic migration, albeit attenuated by the filtering effect of the "sea-mount-hopping" mechanism probably involved.

(d) These results may be taken to imply that, due to former location on the margin of Gondwanaland, both New Zealand and the Sula Islands are now placed on the same side of the winding suturing line between opposite shores of the Tethys.

(e) Analysis of adductor muscle scars patterns may provide important clues for revealing taxonomic relationships of the Nucleatidae, Pygopidae and Discoliidae to a greater degree than previously acknowledged: a superfamily Discoliacea is newly ranked to accomodate the three of them, and the genus *Phymatothyris* is removed from an incertae sedis placement and transferred to the Nucleatinae.

Acknowledgements

The author is deeply indebted to Prof. Derek V. Ager (Swansea), firstly, for stimulative supervising the research project (Ph.D. Thesis) in which many of the background ideas here dealt with started a long mellowing (worthy of a good whisky or a port), secondly, for generously providing access to his personal reference collection of Mesozoic brachiopods and reprints (and for his warm hospitality too), and thirdly, for having remained a constant source of counsel and encouragement ever since.

Studies on the palaeontological collections of the University of Auckland, New Zealand (=AU) were eased by the friendly attitude of Prof. Jack Grant-Mackie and Dr. Joan Sutherland. In addition, the former also collected the type material of the new species described, supplied relevant provenance data, and willingly introduced the author to "kiwi" field stratigraphy of North Island. Likewise, Prof. Gerd Westermann (Hamilton) was the leader of the expedition to the Sula Islands and diligently arranged that some specimens be sent to La Plata Museum (=MLP). Also helpful in this connection was Dr. Susana Damborenea who aided with processing of samples, with determination of bivalves, and with other ancillary matters. Similarly, years ago Drs. Felix Wiedenmayer and Peter Jung kindly allowed examination of C. and O. Renz's material from Greece and Off Morocco at the Basel Museum (=NMB), and Dr. J.-H. Delance showed the writer his fossil collection of Pygopids at Dijon. Travel to New Zealand was funded by the Prince and Princess of Wales Science Award of N.Z. Royal Society (Wellington) and by Antorchas Foundation (Buenos Aires). Help received from these persons and institutions is gratefully acknowledged. Further thanks are due to Rex

Doescher (Washington) for his helpful searchs in the Smithsonian's database, and are also extended to every colleague who has provided reprints of papers through the years.

Appendix 1—Outline of classification referred to in text

Spfam. DISCOLIACEA Fischer et Oehlert, 1891 (Tr?: J–Rc) [nom. trans. herein]

Fam. DISCOLIIDAE Fischer et Oehlert, 1891 (up K?; Tt–Rc) (Cenomanian? Recent)
Sbfam. Discoliinae Fischer et Oehlert, 1891 (Up K–Rc) [n.trans. Cooper, 1983]
Discolia Fischer et Oehlert, 1890 (Pliocene–Recent)
Goniobrochus Cooper, 1983 (Recent)
Waisiuthyrina Beets, 1943 (Tt) (Upper Pliocene or Upp Oligocene)
Moraviaturia Sahni, 1960 (Up K) (Cenomanian)
Sbfam. Aenigmathyridinae Cooper, 1983 (Tt–Rc) (Paleocene-Recent)
Aenigmathyris Cooper, 1971 (Eocene)
Abyssothyris Thomson, 1927 (Miocene–Recent)
Xenobrochus Cooper, 1981 (Recent)
Acrobelesia Cooper, 1983 (Recent)
Ceramisia Cooper, 1983 (Pliocene)
Faksethyris Asgaard, 1971 (Paleocene) (Danian)

Fam. PYGOPIDAE Muir-Wood, 1965 (Jurassic–Cretaceous) [emend. Dieni et al., 1975]
Sbfam. Pygopinae Muir-Wood, 1965 (Upper Jurassic–Lower Cretaceous) [n. trans. Dieni et al., 1975]
Pygope Link, 1830 (Upper Kimmeridgian–Barremian)
(*Antinomia*) Catullo, 1851 (Tithonian–Valanginian?)
Pygites Buckman, 1906 (Upper Tithonian–Lower Barremian)
Sbfam. Triangopinae [nov.] (J–K)
Triangope Dieni et Middlemiss, 1981 (Up Kimmdg? Lw Tithonian–Lw Barremian)
Bolgarithyris Titova, 1986 (Up K) (Maastrichtian)

Fam. NUCLEATIDAE Schuchert in Schuchert et Le Vene, 1929 (Tr?; J–K) [nom.trans. Kamyshan et Babanova, 1973]
Sbfam. Nucleatinae Schuchert in Schuchert et Le Vene, 1929 (Tr?; Lw J–Up K)
Nucleata Quenstedt, 1868–1871 (Md J–Up K) (Bathonian?–Cenomanian)
[=*Glossothyris* Douvillé, 1879]
(*Vjalovithyris*) Tkhorzhevskij, 1989 (Tithonian–Berriasian)
Linguithyris Buckman, 1918 (Lw–Md J) (Sinemurian–Bathonian)
(*Kubanithyris*) Tkhorzhevskij, 1989 (Bajocian)
Phymatothyris Cooper et Muir-Wood, 1951 (Lw J) (Pliensbachian–Toarcian)
[=*Pallasiella* Renz, 1932 non Sars 1895]
Sbfam. Securithyridinae [nov.] (Lw J) (Pliensbachian–Toarcian?)
Securithyris Vörös, 1983 (Pliensbachian)

Spfam. TEREBRATULACEA Gray, 1840 (Tr–Rc)

Fam. TEREBRATULIDAE Gray, 1840 (Tr–Rc)
Sbfam. Nerthebrochinae Cooper, 1983 (J–K)
Sardope Dieni et Middlemiss, 1975 (Lw K)
Sbfam. Aniabrochinae [nov. nom. pro Platythyridinae Dieni et Middlemiss, 1975]
Aniabrochus Cooper, 1983 (Lw K)
[=*Platythyris* Middlemiss, 1959 non Grote et Robinson, 1897]

Fam. TEGULITHYRIDIDAE Muir-wood, 1965 (J)
Tegulithyris Buckman, 1918 (Md J)

Fam. DICTIOTHYRIDIDAE Makridin, 1964 (J)
Dictyothyris Douvillé, 1879

Fam. TRIGONITHYRIDIDAE Radulovic, 1986 (J)
Trigonithyris Muir-Wood, 1935 (J)

References

Ager, D.V., 1959. Lower Jurassic Brachiopods from Turkey. J. Paleontol., 33(6): 1018–1028.

Ager, D.V., 1960. Brachiopod distributions in the European Mesozoic. Rep. Int. Geol. Congr., 21st Sess., Norden, 1960, 22: 20–25.

Ager, D.V., 1963. Principles of Paleoecology. McGraw-Hill, New York, NY, 371 pp.

Ager, D.V., 1965. The adaptation of Mesozoic brachiopods to different environments. Palaeogeogr. Palaeoclimatol., Palaeoecol., 1(2): 143–172.

Ager, D.V., 1967. Some Mesozoic brachiopods in the Tethys region. In: C.G. Adams and D.V. Ager (Editors), Aspects of Tethyan Biogeography. Syst. Assoc. Publ., 7: 135–151.

Ager, D.V., 1968. Brachiopod palaeoecology. Earth-Sci. Rev., 3: 157–179.

Ager, D.V., 1971. Space and time in brachiopod history. In: F.A. Middlemiss, P.F. Rawson and G. Newall (Editors), Faunal Provinces in Space and Time. Geol. J. Spec. Issue, 4: 95–110.

Ager, D.V., 1973. Mesozoic Brachiopoda. In: A. Hallam (Editor), Atlas of Palaeobiogeography. Elsevier, Amsterdam, pp. 431–436.

Ager, D.V., 1974. The western High Atlas of Morocco and their significance in the history of the North Atlantic. Proc. Geol. Assoc., 85(1): 23–41.

Ager, D.V., 1975. Brachiopods at the Jurassic–Cretaceous boundary. In: Colloque sur la limite Jurassique–Crétace, Lyon, 1973. Mém. Bur. Rech. Geol. Min., 86: 150–162.

Ager, D.V., 1976. The nature of the fossil record. Proc. Geol. Assoc., 87(2): 131–159.

Ager, D.V., 1979. The stratigraphical distribution of Jurassic

Brachiopoda. In: A Collection of Papers in Honour of Professor G.W. Chiplonkar. Recent Res. Geol. Delhi, 4: 6–21.

Ager, D.V., 1980. The Geology of Europe. Mc Graw-Hill, New York, NY, 535 pp.

Ager, D.V., 1981. Major marine cycles in the Mesozoic. J. Geol. Soc. London, 138: 159–166.

Ager, D.V., 1986a. Evolutionary patterns in the mesozoic brachiopoda. In: P.R. Racheboeuf and C.C. Emig (Editors), Les Brachiopodes Fossiles et Actuels. Biostratigr. Palèoz., 4: 33–41.

Ager, D.V., 1986b. Migrating fossils, moving plates and an expanding Earth. Mod. Geol., 10: 377–390.

Ager, D.V., 1990. British Liassic Terebratulida (Brachiopoda). Part 1. Monogr. Palaeontogr. Soc., London, 143(582): 1–39.

Ager, D.V., 1991. Faunal replacements in benthic communities. Atti Quarto Simp. Ecol. Paleoecol. Comun. Benton., Mus. Region. Sci. Nat. Torino, pp. 11–20.

Ager, D.V. and Sun, D.-L., 1988. Distribution of Mesozoic-brachiopods on the northern and southern shores of Tethys. Palaeontol. Cathayana, 4: 23–51.

Ager, D.V. and Walley, C.D., 1977. Mesozoic brachiopod migrations and the opening of the North Atlantic. Palaeogeogr., Palaeoclimatol., Palaeoecol., 21(2): 85–99.

Audley-Charles, M.G., 1981. Geological history of the region of Wallace's Line. In: T.C. Whitmore (Editor), Wallace's Line and Plate Tectonics. Clarendon Press, Oxford, pp. 24–35.

Barczyk, W., 1969. Upper Jurassic Terebratulids from the Mesozoic border of the Holy Cross Mountains in Poland. Pr. Muz. Ziemi, 14: 3–82.

Barczyk, W., 1972. On the representatives of the genus *Nucleata* Quenstedt (Brachiopoda) from the Tithonian and Berriasian of theenvirons of Czorsztyn, Poland. Pr. Muz. Ziemi, 20: 151–160.

Basse, E., 1930. Contribution á l'étude du Jurassique supérieur (Facies Corallien) en Ethiopie et en Arabie méridionale. Mém. Soc. Géol. Fr., 14, N. S., 6(3–4): 105–148.

Blanchet, F., 1929. Etude palèontologique d'un nouveau gisement fossilifère dans le Tithonique intra-alpin entre Briançon et Chateau Queyras. Trav. Lab. Geol. Fac. Sci. Grenoble, 15(1): 48–85.

Böse, E., 1893. Die Fauna der liasischen Brachiopodenschichten bei Hindelang (Algäu). Jahrb. K. K. Geol. Reichsanst., 42(4): 627–650.

Böse, E., 1897. Die mittelliasische Brachiopodenfauna der östlichen Nordalpen. Nebst einem Anhange über die Fauna des unteren Dogger im bayerischen Innthale. Palaeontographica, 44(3–4): 145–235.

Böse, E. and Finkelstein, H., 1892. Die mitteljurassischen Brachiopoden-Schichten bei Castel Tesino im östlichen Südtyrol. Z. Dtsch. Geol. Ges., 44(2): 265–302.

Boullier, A., 1981. Les faunes de brachiopodes de l'Oxfordien moyen du Jura. Ann. Sci. Univ. Besançon Geol., Ser. 4, 3: 21–31.

Brambilla, G., 1971. Alcuni fossili domeriani delle Prealpi lombarde. Natura, Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Acquario Civ. Milano, 62(4): 467–478.

Brower, J.C. and Veinus, J., 1978. Multivariate analysis of allometry using point coordinates. J. Paleontol., 52(5): 1037–1053.

Buckman, S.S., 1906. Brachiopod Homoeomorphy: *Pygope*, *Antinomia*, *Pygites*. Q. J. Geol. Soc., 62(3): 433–455.

Buckman, S.S., 1918. The Brachiopoda of the Namyau Beds, Northern Shan States, Burma. Mem. Geol. Surv. India, Palaeontol. Indica N. S., 3(2): 1–254.

Calzada Badía, S., 1985. Braquiópodos del Hauteriviense de Fortuna (Prov. Murcia, España). Boll. Soc. Ital., 23(1): 75–90.

Canavari, M., 1880. La Montagna del Suavicino. Boll. Com. Geol. Ital., 11: 54–73; 254–264.

Canavari, M., 1881. Alcuni nuovi brachiopodi degli strati a *Terebratula aspasia* Mgh. nell'Appennino centrale. Atti Soc. Toscana Sci. Nat. Pisa Mem., 5(1): 177–188.

Canavari, M., 1882. Beträge zur Fauna des unteren Lias von Spezia. Palaeontographica N. F., 9(3): 125–192.

Canavari, M., 1883. Contribuzione III alla conoscenza dei Brachiopodi degli strati a *Terebratula aspasia* Mgh. nell' Appennino Centrale. Atti Soc. Toscana Sci. Nat. Pisa Mem., 6(1): 70–110.

Choffat, P., 1880. Etude stratigraphique et palèontologique des terrains jurassiques du Portugal. Première livraison. Le Lias et le Dogger au Nord du Tage. Mem. Sec. Trab. Geol. Port., Lisboa, 72 pp.

Choffat, P. , 1947. Description de la Faune Jurassique de Portugal. Brachiopodes. Serv. Géol. Port., pp. 1–46.

Cooper, G.A., 1983. The Terebratulacea (Brachiopoda), Triassic to Recent: A study of the brachidia (loops). Smithson. Contrib. Paleobiol., 50: 1–445.

Dacqué, E., 1905. Beiträge zur Geologie des Somalilandes. Zweiter Teil. Oberer Jura. Beitr. Paläontol. Geol. Oest.-Ung., 17: 119–159.

Dal Piaz, G., 1907. Sulla fauna Liasica delle Tranze de Sospirolo. Parte Prima. Mém. Soc. Paléontol. Suisse, 33: 1–64.

Damborenea, S.E., 1990. Middle Jurassic inoceramids from Argentina. J. Paleontol., 64(5): 736–759.

Dareste de la Chavanne, J., 1920. Fossiles liasiques de la région de Guelma. Matér. Carte Géol. Algérie, 1 sér., Paléontol., 5: 1–72.

Dareste de la Chavanne, J., 1930. Monographie paléontologique de faunes liasiques et jurassiques du Maroc nord-oriental. Notes Mém. Serv. Min. Carte Géol. Morocco, 16: 31–100.

De Brun, P., and Marcelin, P. , 1934. Etude stratigraphique des Petits Causses des environs de Florac (Lozére). Bull. Soc. Hist. Nat. Toulouse, 66(3–4): 377–491.

De Gregorio, A., 1930. Monografia dei fossili Liassici di Monte San Giuliano conservati nel mio privato gabinetto geologico. Ann. Géol. Paléontol. Palermo, 53: 1–57.

De Grossouvre, A., 1891. Sur le Callovien de l'Ouest de la France et sur sa faune. Bull. Soc. Géol. Fr., Sér. 3, 19: 247–262.

Dieni, I. and Middlemiss, F.A., 1981. Pygopid brachiopods from the Venetian Alps. Boll. Soc. Paleontol. Ital., 20(1): 19–48.

Dieni, I., Middlemiss, F.A. and Owen, E.F., 1975. The Lower Cretaceous Brachiopods of east-central Sardinia. Boll. Soc. Paleontol. Ital., 12(2): 166–216.

D'Orbigny, A., 1850. Paléontologie Française. Terrains Crétacés. Paris, 4, 390 pp.

Dubar, G., 1931. Lias et jurassique du Baztan (Haute Vallée de la Bidassoa—Espagne). Bull. Soc. Géol. Fr. Ser. 4, 30: 589–608.

Dubar, G., 1950. Sur des Faunes de Brachiopodes du Lias Supérieur dans les fentes du Domérien supérieur au djebel Bou-Dahar (Haut-Atlas marocain). Ann. Soc. Géol. Nord, 70: 205–213.

Dubar, G., 1962. Notes sur la paléogéographie du Lias marocain (Domaine Atlasique). In: Livre Mém. P. Fallot. Mém. Soc. Géol. Fr., pp. 529–544.

Dulai, A., 1990. The Lower Sinemurian (Jurassic) brachiopod fauna of the Lókút Hill (Bakony Mts., Hungary). Preliminary results. Ann. Hist.-Nat. Mus. Natl. Hung., 82: 25–37.

Dumortier, E., 1874. Etudes Paléontologiques sur les Dépots Jurassiques du Bassin du Rhone. 4. Lias Supérieur. Savy, Paris, 335 pp.

Elmi, S. and Alméras, Y., 1984. Physiography, palaeotectonics and palaeoenvironments as controls of changes in ammonite and brachiopod communities (an example from the Early and Middle Jurassic of western Algeria). Palaeogeogr., Palaeoclimatol., Palaeoecol., 47: 347–360.

Favre, E., 1875. Description des fossiles du terrain jurassique de la Montagne des Voirons (Savoie). Mém. Soc. Paléontol. Suisse, 2(2): 1–79.

Favre, E., 1876. Description des fossiles du terrain oxfordien des Alpes fribourgeoises. Mém. Soc. Paléontol. Suisse, 3(2): 1–76.

Favre, E., 1877. La Zone a Ammonites acanthicus dans les Alpes de la Suisse et de la Savoie. Mém. Soc. Paléontol. Suisse, 4(3): 1–115.

Favre, E., 1880. Description des fossiles des couches tithoniques des Alpes fribourgeoises. Mém. Soc. Paléontol. Suisse, 6(1): 1–75.

Ferrari, A. and Manara, C., 1972. Brachiopodi del Dogger inferiore di Monte Peller—Trentino. G. Geol. (Ann. Mus. Geol. Bologna), Ser. 2, 38(1): 253–348.

Flamand, G., 1911. Recherches géologiques et géographiques sur le Haut-Pays de l'Oranie et sur le Sahara (Algérie et territoires du Sud). Thesis. Univ. Lyon, 47, 1001 pp.

Fleming, C., 1967. Biogeographic change related to Mesozoic orogenic history in the southwest Pacific. Tectonophysics, 4(4–6): 419–427.

Fucini, A., 1896. Fauna del Lias medio del Monte Calvi presso Campiglia Maritima. Palaeontogr. Ital. Mem. Paleontol., 2: 203–250.

Fucini, A., 1920. Fossili domeriani dei dintorni di Taormina. Palaeontogr. Ital. Mem. Paleontol., 26: 75–116.

Fülop, J., 1964. A Bakonyhegység Alsó-Kreta (Berriázi–Apti) képződményei. Geol. Hung., 13: 1–194 (in Hungarian).

Gemmellaro, G.G., 1874. Sopra i fossili della zona con *Terebratula aspasia*, Menegh. della provincia di Palermo e di Trapani. G. Sci. Nat. Econ. Palermo, 10: 73–132.

Gemmellaro, G.G., 1876. Studi paleontologici sulla fauna del calcare a "*Terebratula Janitor*" del Nord della Sicilia. III. G. Sci. Nat. Econ. Palermo, 7: 74–149.

Geyer, G., 1889. Ueber die liasische Brachiopodenfauna des Hierlatz bei Hallstatt. Abhl. K. K. Geol. Reichanst., 15(1): 1–88.

Geyer, O.F., 1967. Zur faziellen Entwicklung des subbetisches Juras in Südspanien. Geol. Rundsch., 56(3): 973–991.

Geyssant, J., 1966. Etude paléontologique des faunes du Jurassique supérieur de la zone prérifaine du Moyen Ouerrha. Première partie. *Glossothyris* et *Pygope* (Terebratulidae). Essai de répartition de ces espèces dans le domaine méditerranéen. Notes Serv. Géol. Maroc., 26(188): 75–102.

Geyssant, J. and Mascle, G., 1970. Deux gisements fossilifères du Tithonique des monts Sicani (Sicile occidentale). C.R. Somm. Seanc. Soc. Géol. Fr., 6: 213–214.

Gočanin, M., 1938. Ueber die fossilführenden Schichten Kimmeridgien, Tithon, Valanginien und Hauterive aus der Umgebung von Beograd. Vesn. Geol. Inst. Kralj. Jugoslav., 6: 35–71.

Grant-Mackie, J., 1985. New Zealand–New Caledonian Permian–Jurassic faunas, biogeography and terranes. N. Z. Geol. Surv. Rec., 9: 50–52.

Haq, B.U., Hardenbol, J. and Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic. Science, 235: 1156–1167.

Hayami, I., 1984. Jurassic marine bivalve faunas and biogeography in Southeast Asia. Geol. Palaeontol. Southeast Asia, 25: 229–237.

Hayami, I., 1987. Geohistorical background of Wallace's line and Jurassic marine biogeography. In: A. Taira and M. Tashiro (Editors), Historical Biogeography and Plate Tectonic Evolution of Japan and Eastern Asia. Terrapub, Tokyo, pp. 111–133.

Horwitz, L., 1939. Bathonien, Callovien, Oxfordien et Argovien dans le massif de Bruns (Fribourg). Bull. Soc. Vaudoise Sci. Nat., 60(250): 351–438.

Jarre, P. , 1962. Révision du genre *Pygope*. Trav. Lab. Géol. Fac. Sci. Grenoble, 38: 23–120.

Jekelius, E., 1915. Die mesozoischen Faunen der Berge von Brassó. II. Die Neokomfauna von Brassó. Mitt. Jahrb. K. Ung. Geol. Reichsanst., 23(2): 114–136.

Jimenez de Cisneros, D., 1923. La fauna de los estratos de "Pygope Aspasia" Menegh. del Liásico medio del Rincón de Egea, en el NW. de la provincia de Murcia. Trab. Mus. Nac. Cienc. Nat. Ser. Geol., 30: 1–55.

Jimenez de Cisneros, D., 1935. La Fauna Liásica de los Cerros de Ayala y de la Cruz de la Algueña en la parte occidental de la provincia de Alicante. Mem. Soc. Ibér. Cienc. Nat., 7: 1–31.

Kamyshan, V.P. and Babanova, L.I., 1973. Sredneyurskie i Pozdneyurskie Brakhiopody Severo-Zapadnogo Kavkaza i Gornogo Kryma. Izdatel. Obshch. V. Shkola Izd. Khar'kov Gosud. Univ., Kharkov, 175 pp. (in Russian).

Ksiäzkiewicz, M., 1956. Jura i Kreda Bachowic. Ann. Soc. Géol. Pologne, 24(2–3): 119–405 (in Polish, with English summary).

Laurin, B., 1979. Convergence morphologique entre les brachiopodes sulqués: *Septocrurella sanctae-clarae* (Roemer)—Rhynchonellacea, Erymnariidae—et *Nucleata nucleata* (Schlotheim) —Terebratulacea, Pygopidae—dans l'Oxfordien de la région d'Aiglun (Alpes Maritimes). Géol. Médit., 6(3): 417–422.

Lillo Beviá, J., 1977. Sobre algunos braquiópodos de la Sierra de Crevillente (Alicante). Bol. R. Soc. Esp. Hist. Nat. (Geol.), 74(1–4): 81–95.

Makridin, V.P. , 1964. Brakhiopody Yurskikh otlozhenij Russkoj Platformy i nekotorykh prilezhashchikh k nej oblastej. Gorkii-Kharkov State Univ. Sci. Res. Sect., Izd-vo Nedra, Moscow, 395 pp. (in Russian).

Malinowska, L., 1967. Biostratygrafia osadów Dolnego iSrodkowego Oksfordu Obrzezenia gór Swietokrzyskich. Biul. Inst. Geol., 3(209): 53–112 (in Polish, with English summary).

Manceñido, M.O., 1978. Studies of Early Jurassic Brachiopoda and their distribution, with special reference to Argentina. Thesis. Dep. Geol. Univ. Coll. Swansea, Univ. Wales, 481 pp. (unpubl.).

Marques, B. and Rocha, R.B., 1981. Formações jurássicas da região de Albufeira: estratigrafia, consequencias cartográficas e tectónicas. Univ. Nova Lisboa, Cienc. Terra, 6: 39–48.

Masse, J.P., 1992. The Lower Cretaceous Mesogean benthic ecosystems: palaeoecologic aspects and palaeobiogeographic implications. Palaeogeogr., Palaeoclimatol., Palaeoecol., 91(3–4): 331–345.

Metcalfe, I., 1991. Late Palaeozoic and Mesozoic palaeogeography of Southeast Asia. Palaeogeogr., Palaeoclimatol., Palaeoecol., 87(1–4): 211–221.

Middlemiss, F.A., 1973. The geographical distribution of Lower Cretaceous Terebratulacea in Western Europe. In: R. Casey and P. Rawson (Editors), The Boreal Lower Cretaceous. Geol. J. Spec. Issue, 5: 111–120.

Middlemiss, F.A., 1984. Distribution of Lower Cretaceous Brachiopods and its relation to climate. In: P. Brenchley (Editor), Fossils and Climate. Wiley, New York, pp. 165–170.

Moiseev, A.S., 1934. Brakhiopody Yurskikh otlozhenii Kryma i Kavkaza. Tr. Vses. Geol. Razved. Ob'edin. NKTP SSSR, 203: 1–216 (in Russian and English).

Moiseev, A.S., 1947. Klass Brachiopoda. Plechenogie. In: G. Krymgol'ts (Editor), Atlas rukovodyashikh form iskopaemoj fauny SSSR. 3. Nizhnij i srednij otdely yurskoj sistemy. Gosgeolizdat, pp. 83–102 (in Russian).

Mouterde, R., Rocha, R.B., Ruget, C. and Tintant, H., 1979. Facie's, biostratigraphie et paléogéographie du jurassique portugais. Univ. Nova Lisboa, Cienc. Terra, 5: 29–51.

Muir-Wood, H.M., 1965. Mesozoic and Cenozoic Terebratulidina. In: R.C. Moore (Editor), Treatise on Invertebrate Paleontology. Part H. Brachiopoda. Geol. Soc. Am. and Univ. Kansas Press, 2, pp. H762–H816.

Nekvasilova, O., 1980. Terebratulida (Brachiopoda) from the Lower Cretaceous of Stramberk (north-east Moravia), Czechoslovakia. Sb. Geol. Ved (Paleontol.), 23: 49–81.

Nicolis, E. and Parona, C.F., 1885. Note stratigrafiche e paleontologiche sul Giura superiore della Provincia di Verona. Boll. Soc. Geol. Ital., 4: 1–96.

Oppel, A., 1861. Ueber die Brachiopoden des untern Lias. Z. Dtsch. Geol. Ges., 13(4): 529–550.

Owen, E.F., 1976. Some Lower Cretaceous brachiopods from East Greenland. Meddel. Grønl., 171(3): 1–19.

Parona, C.F., 1883. Contributo allo studio della fauna liasica dell'Apennino centrale. Atti R. Accad. Lincei Ser. 3, 15: 643–674.

Parona, C.F., 1885. I brachiopodi liassici di Saltrio e Arzo nelle Prealpi lombarde. Mem. R. Inst. Lomb. Sci. Lett., Cl. Sci. Mat. Nat., 15: 227–262.

Parona, C.F., 1892. Revisione della fauna liasica di Gozzano in Piemonte. Mem. R. Accad. Sci. Torino, Ser. 2, 43: 1–62.

Parona, C.F. and Canavari, M., 1882. Brachiopodi oolitici di alcune località dell'Italia Settentrionale. Atti Soc. Toscana Sci. Nat. Pisa, Mem., 5(2): 331–350.

Peybernès, B. and Calzada Badía, S., 1981. *Orbirhynchia memii* n.sp. et *Nucleata burolleti* n. sp. , brachiopodes nouveaux du Cenomanien de la région de la Kessera (Tunisie centrale). Notes Serv. Geol. Tunis, 46: 61–72.

Principi, P. , 1910. Brachiopodi del Lias Medio di Castel del Monte (presso Acquasparta). Riv. Ital. Paleontol., 16(3): 63–88.

Prozorovskaya, E., 1985. Brakhiopody. In: K.O. Rostovtsev (Editor), Yurskie Otlozheniya Yuzhnoj Chasti Zakavkaz'ya. Izd-vo Nauka, Leningrad, pp. 45–49; 101–118; 181–183 (in Russian).

Quenstedt, F.A., 1856–1857. Der Jura. Laupp'fchen, Tübingen, 842 pp.

Quenstedt, F.A., 1868–1871. Petrefaktenkunde Deutschlands. Zweiter Band. Die Brachiopoden. Fues's, Leipzig, pp. 1–160 (1868); 161–464 (1869); 465–748 (1870); plates (1871).

Radulovic, V., 1986. A new family and genus of Terebratulida (Brachiopoda) from the Upper Bajocian–Bathonian of the Yugoslavian Carpatho-Balkanides. Senckenbergiana Lethaea, 67(1–4): 43–53.

Rau, K., 1905. Die Brachiopoden des mittleren Lias Schwabens mit Ausschluss der Spiriferinen. Geol. Paläontol. Abh., 10(5): 263–355.

Renz, C., 1932. Brachiopoden des südschweizerischen und westgriechischen Lias. Abh. Schweiz. Paläontol. Ges., 52: 1–61.

Renz, O., Imlay, R., Lancelot, Y. and Ryan, W.B.F., 1975. Ammonite-rich Oxfordian limestones from the base of the continental slope off northwest Africa. Eclogae Geol. Helv., 68(2): 431–448.

Retowski, O., 1894. Die Tithonischen Ablagerungen von Theodosia. Ein Beitrag zur Paläontologie der Krim. Bull. Soc. Imp. Nat. Moscow, N. S., 7: 276–289.

Richardson, J.R., 1981. Brachiopods in mud: resolution of a dilemma. Science, 211(4487): 1161–1163.

Rollier, L., 1918. Synopsis des Spirobranches (Brachiopodes) Jurassiques Celto-Souabes. Troisième Partie (Terébratulidés). Mém. Soc. Paleontol. Suisse, 43: 185–275.

Rothpletz, A., 1886. Geologisch-palaeontologische Monographie der Vilser Alpen, mit besonderer Berücksichtigung der Brachiopoden-Systematik. Palaeontographica, 33(1–3): 1–180.

Rudwick, M.J.S., 1970. Living and Fossil Brachiopods. (Biol. Sci., 147). Hutchinson, London, 199 pp.

Sacchi-Vialli, G. and Cantaluppi, G., 1967. I nuovi fossili di Gozzano (Prealpi Piemontesi). Mem. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano, 16(2): 61–127.

Sandy, M.R., 1991. Aspects of Middle–Late Jurassic–Cretaceous Tethyan brachiopod biogeography in relation to tectonic and paleoceanographic developments. Palaeogeogr., Palaeoclimatol., Palaeoecol., 87(1–4): 137–154.

Scotese, C.R., 1991. Jurassic and Cretaceous plate tectonic reconstructions. Palaeogeogr., Palaeoclimatol., Palaeoecol., 87(1–4): 493–501.

Sequeiros, L., 1977. Nuevos datos paleontológicos y bioestratigráficos de *Glossothyris* (Brachiopoda, Terebratulidae) en la zona subbética (España meridional). Acta Geol. Hisp., 12(1–3): 8–11.

Siblík, M., 1964. K nálezu Liasovy'ch brachiopodu v horní části Belanská Doliny. Geol. Práce Zprávy, 31: 157–181 (in Czech, with English abstract).

Siblík, M., 1966. Ramenonoczi Kosteleckého Bradla. Geol. Práce Zprávy, 38: 137–157 (in Czech, with English abstract).

Siblík, M., 1967. New species of Domerian rhynchonelloids from Slovakia. Geol. Sb., 18(1): 151–168.

Smirnova, T.N., 1972. Rannemelovye Brakhiopody Kryma i severnogo Kavkaza. Nauka, Moscow, 143 pp. (in Russian).

Smith, A.G. and Briden, J.C., 1977. Mesozoic and Cenozoic Paleocontinental Maps. Cambridge Univ. Press, Cambridge, 63 pp.

Steinmann, G., 1925. Gibt es fossile Tiefseeablagerungen von erdgeschichtlicher Bedeutung ? Geol. Rundsch., 16(6): 435–468.

Stevens, G.R., 1990. The influences of palaeogeography, tectonism and eustasy on faunal development in the Jurassic of New Zealand. Atti 2nd Conv. Int. Fossili, Evoluzione, Ambiente. Pergola, 25–30 ottobre 1987, pp. 441–457.

Taddei-Ruggiero, E. and Vörös, A., 1987. Paleobiogeographical evaluation of Calabrian Liassic brachiopods. Rend. Soc. Geol. Ital., 9: 235–242.

Tchoumatchenco, P.V., 1978. Brakhiopodi ot kalovskiya etazh i gornoyurskata seriya na chast ot Zapadniya Predbalkan. Bulg. Acad. Sci. Paleontol. Stratigr. Litol., 8: 3–54 (in Bulgarian, with French resumé).

Tchoumatchenco, P.V., 1986. Répartition paléoécologique des Brachiopodes jurassiques dans les monts de Tiaret et l'Ouarsenis occidental (Algérie). In: P.R. Racheboeuf and C.C. Emig (Editors), Les Brachiopodes Fossiles et Actuels. Biostratigr. Paléoz., 4: 389–398.

Tchoumatchenco, P.V., 1990. Brachiopodes jurassiquess inférieurs et moyens des olistolithes inclus dans la Formation de Kotel (Jurassique moyen) (Stara planina orientale, Bulgarie). II. Spiriferida, Terebratulida. Bulg. Acad. Sci. Paleontol. Stratigr. Litol., 28: 3–40.

Termier, H. and Termier, G., 1956. La notion de migration en paléontologie. Geol. Rundsch., 45(1): 26–42.

Thayer, C.W., 1981. Ecology of living brachiopods. In: J.T. Dutro and R.S. Boardman (Editors), Lophophorates. Notes for a Short Course. Univ. Tennessee, Dep. Geol. Sci., Stud. Geol., 5: 110–126.

Titova, M.V., 1986. Novye Pozdnemelovye Terebratulidy. Paleontol. Zh., 1986(1): 117–124.

Titova, M.V., 1992. Brakhiopody verkhnego Mela Yuga SSSR. Tr. VSEGEI, N. S., 350: 137–171.

Tkhorzhevskij, Eh.S., 1989. O Yurskikh terebratulidakh Nucleatidae (Brakhiopody). Paleontol. Zh., 1989(4): 25–36.

Tkhorzhevskij, Eh.S. and Radulovicj, V., 1984. Novi podatsi o srednje jurskim terebratulidama (Brachiopoda) Karpata (SSSR) i Karpato-Balkanida (Jugoslavija). Ann. Géol. Pénin. Balkan., 48: 129–184 (in Serbian, with English summary).

Uhlig, V., 1879. Ueber die liasische Brachiopodenfauna von Sospirolo bei Belluno. Sitzungsber. Akad. Wiss. Wien, 8(1): 259–310.

Uhlig, V., 1881. Ueber die Fauna des rothen Kellowaykalkes der penninischen Klippe Babierżowka bei Neumarkt in Westgalizien. Jahrb. K. K. Geol. Reichsanst., 31: 381–422.

Vigh, G., 1943. A Gerecse hegység Eszaknyugati részének földtani és öslénytani viszonyai. Föld. Közl., 73(4–9): 301–359; 537–550 (in Hungarian, with German abstract).

Vogel, K., 1966. Eine funktionsmorphologische Studie an der Brachiopodengattung *Pygope* (Malm bis Unterkreide). Neues Jahrb. Geol. Paläont., Abh., 125: 423–442.

Vogel, K., 1986. Origin and diversification of brachiopod shells: viewpoints of constructional morphology. In: P.R. Racheboeuf and C.C. Emig (Editors), Les Brachiopodes Fossiles et Actuels. Biostratigr. Paléoz., 4: 399–408.

Vörös, A., 1973. Speculations on food supply and bathymetry in the Mediterranean Jurassic sea. Ann. Univ. Sci. Budapest. R. Eötvös Nom., Sect. Geol., 16: 214–221.

Vörös, A., 1975. Bathymetric distribution of some Mediterranean Lower Jurassic brachiopods (Bakony Mountains, Hungary). Ann. Univ. Sci. Budapest. R. Eötvös Nom., Sect. Geol., 17: 279–286.

Vörös, A., 1977. Provinciality of the Mediterranean Lower Jurassic brachiopod fauna: causes and plate tectonic implications. Palaeogeogr., Palaeoclimatol., Palaeoecol., 21(1): 1–16.

Vörös, A., 1980. Liász és dogger brachiopoda provinciák a Nyugati-Tethysben. Föld. Közl., 110(3–4): 395–416 (in Hungarian, with English abstract).

Vörös, A., 1983. Some new genera of Brachiopoda from the Mediterranean Jurassic. Ann. Hist. Nat. Mus. Natl. Hung., 75: 5–25.

Vörös, A., 1984a. Lower and Middle Jurassic brachiopod provinces in the western Tethys. Ann. Univ. Sci. Budapest. R. Eötvös Nom., Sect. Geol., 24: 207–233.

Vörös, A., 1984b. Comparison of Jurassic benthonic mollusc and brachiopod faunas of the Transdanubian Mountains (Hungary). Acta Geol. Hung., 27(3–4): 391–401.

Vörös, A., 1986. Brachiopod palaeoecology on a Tethyan Jurassic seamount (Pliensbachian, Bakony Mountains, Hungary). Palaeogeogr., Palaeoclimatol., Palaeoecol., 57(4): 241–271.

Vörös, A., 1987. Pliensbachian brachiopod biogeography of the "Mediterranean microcontinent". Acta Geol. Hung., 30(1/2): 59–80.

Vörös, A., 1990. Liász és Dogger Brachiopoda-elterjedési adatok az Alp-Kárpáti régió ősföldrajzi értékeléséhez. Altalános Föld. Szemle, 25: 251–263 (in Hungarian, with English abstract).

Vörös, A., Pevny, J., Prosorovskaya, E.L., Sandy, M.R., Middlemiss, F.A. and Smirnova, T.N., 1988. Paleobiology of the Brachiopoda. In: J. Dercourt and A.E.M. Nairn (Editors), Evolution of the Northern Margin of the Tethys. I. Mém. Soc. Géol. Fr. N. S., 154: 45–91.

Westermann, G.E.G., Sato, T. and Skwarko, S.K., 1978. Brief report on the Jurassic biostratigraphy of the Sula Islands, Indonesia. Newsl. Stratigr., 7(2): 96–101.

Wiedenmayer, F., 1963. Obere Trias bis mittlerer Lias zwischen Saltrio und Tremona (Lombardische Alpen). Die Wechselbeziehungen zwischen Stratigraphie, Sedimentologie und syngenetischer Tektonik. Eclogae Geol. Helv., 56(2): 529–640.

Zittel, K.A., 1869. Geologische Beobachtungen aus den Central-Apenninen. Geognost. Paläontol. Beitr., 2(2): 91–177.

Zittel, K.A., 1870. Fauna der aeltern Cephalopodenfuehrenden Tithonbildungen. Palaeontographica Suppl., 2, 309 pp.