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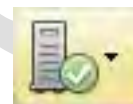
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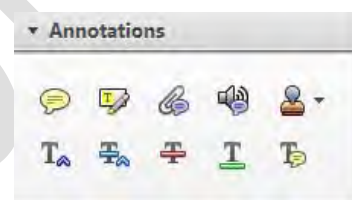


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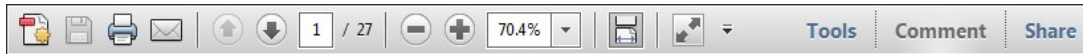


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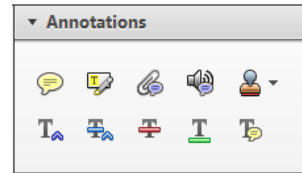
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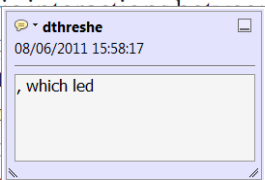


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standard framework for the analysis of microeconomic activity. Nevertheless, it also led to the development of a number of strategic approaches to the analysis of the number of competitors in an industry. This is that the strategic components of an industry, which led to the emergence of the main components of an industry, are exogenous. The important words on entry by Shirone (M henceforth) we open the 'black b



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there is no room for extra profits as mark-ups are zero and the number of firms (net) values are not determined by market structure. Blanchard ~~and Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply shocks in a classical framework assuming monopoly. An exogenous number of firms

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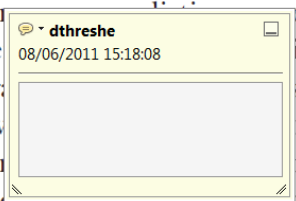


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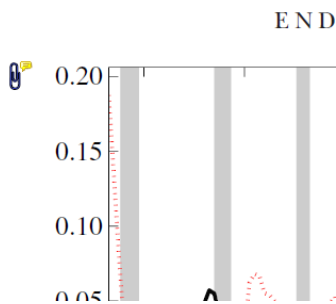
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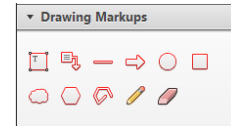
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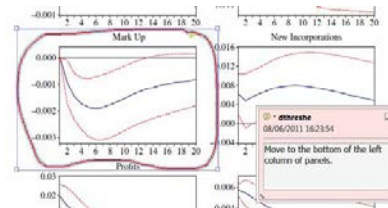
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Oppelzones and their heritage in current larger foraminiferal biostratigraphy

JOHANNES PIGNATTI  AND CESARE A. PAPAZZONI

LETHAIA



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The Oppelzone remains a controversial topic in stratigraphy, despite the attempts to systematize biozonal units in the *International Stratigraphic Guide* (ISG). In the first edition of the ISG, the Oppelzone was regarded as a particular kind of biozone, although with boundaries were recognized as ‘difficult to define empirically’. This is probably the main reason why the Oppelzone was removed from the second edition of the ISG. Here, we review briefly the history and significance of the Oppelzone, starting from Jurassic zonal biostratigraphy as introduced by Oppel himself, and based mainly on ammonites, to its present usage, distinguishing the multiple meanings of the unit – biostratigraphical, chronostratigraphical, or even as a time interval. We review the Oppelzone as integral part of the current biostratigraphy of Palaeogene–Miocene larger foraminifera (the Shallow Benthic Zones, SBZ). Here, different species concepts in individual systematic groups result either in Opeelian (e.g. nummulitids, alveolinids) or non-Opeelian (e.g. lepidocyclinids, miogypsinids and in part orthophragmines) biozones. In addition, various regional larger foraminiferal zonations have been established. These different kinds of biozones are subsumed under the biochronostratigraphic SBZ system in a similar way as regional ammonite zonations are integrated in the standard ammonite zonation. To overcome issues of fuzzy-defined boundaries, a novel research programme is needed to (1) establish the most suitable markers for biozonal boundaries; (2) enhance correlation with different systematic groups (especially planktonic foraminifera and calcareous nannofossils) and with other stratigraphical tools (magnetostratigraphy, radiometric dating, isotopic stratigraphy, etc.); and (3) extend morphometric criteria wherever possible to recognize the markers themselves. □ *Biostratigraphy, chronostratigraphy, larger foraminifera, Oppelzone, Palaeogene.*

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Contrary to common opinion – as set forth in international stratigraphical guides and national codes – Opeelian zones, whether biostratigraphical or chronostratigraphical, are still currently employed in the stratigraphical use of important fossil groups, such as Mesozoic ammonites and Cenozoic larger foraminifera. The primary aim of this article was to discuss the different interpretations that have been put forward on the subject of Oppelzones, highlighting similarities and differences in these two groups. After addressing this issue, we review the current state of larger foraminiferal biozonation and biochronology and discuss future perspectives.

The dual nature of Oppelzones

Albert Oppel (1831–1865) is remembered as one of the founders of the discipline of biostratigraphy or zonal stratigraphy, as applied in his *Juraformation* (1856–1858) (Hancock 1977). A comprehensive

review of his outstanding scientific work is given in Balini *et al.* (2017). Yet, Oppel’s zonal concept, interpreted and named in different ways, such as ‘Oppel’s zone’ (Arkel 1956), ‘Oppel zone’ (e.g. Salvador 1994), ‘Oppel-zone’ (Hedberg 1976), ‘Opeelian Zone’ (Callomon 1994), ‘Oppelzone’ or ‘oppelzone’ (e.g. Carter 2007), ‘Oppel fossilzone’ (Walsh 1998) and ‘Oppel biochron’ (Walsh 1998), has given rise to radically different interpretations.

These different interpretations arise from a basic dichotomy, that is whether Oppel’s zone (hereafter: Oppelzone) should be considered as a particular kind of biozone (Hedberg 1976), or as a particular kind of chronostratigraphical (biochronological) unit (e.g. Arkel 1956; Callomon 1994, 1995; Fig. 1). Arkel (1956, p. 5) even hinted at a third interpretation, namely that an Oppelzone could be a time interval, although this inference is not discussed further here, because, as stated earlier by the same author, ‘before 1893 (...) we find no attempt to formulate any strictly chronological ideas, or to

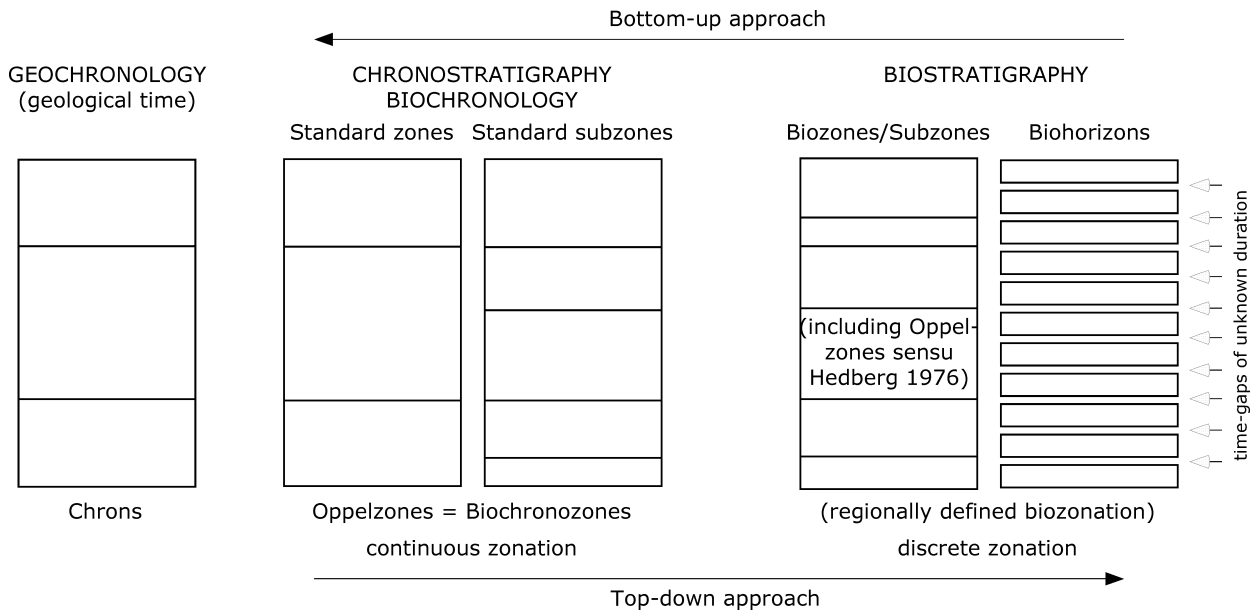


Fig. 1. Bottom-up or top-down approaches to Oppelzones in ammonite biostratigraphy.

construct a time-scale independent of strata (...). No vocabulary for any such conceptions existed' (Arkell 1933, p. 19).

In the same work, Arkell (1933, p. 17) defined the Oppelzone as a biozonal unit, that is as 'a bed or group of beds, identified by palaeontological criteria (by a fossil or an assemblage of fossils)'. This definition is very broad, because it accommodates most kinds of biozones, as presently understood; also, it suggests that an Oppelzone may be characterized either by a single taxon, or by an assemblage of taxa, albeit there is little doubt that in Arkell's (1933) interpretation emphasis is on an assemblage. Finally, Arkell (1933) emphasized that Oppelzones should be considered as biostratigraphical and not chronostratigraphical units, although later he espoused a different view (Arkell 1956).

The concept of Oppelzone as a particular biostratigraphical unit was further circumscribed by Hedberg (1976, p. 58) in the first edition of the *International Stratigraphic Guide* (ISG). Hedberg considered the Oppelzone as one of the main categories of range biozones, that is 'a zone characterized by an association or aggregation of selected taxa [sic] of restricted and largely concurrent range, chosen as indicative of approximate contemporaneity. Not all of the taxa considered diagnostic need be present at any one place for the zone to be legitimately identified. The lower part of the zone is commonly marked largely by first appearance and its upper part by last appearance of certain taxa. The body of the zone is marked largely by concurrences of the diagnostic taxa.' He also recognized its

peculiar subjective character, inasmuch an Oppelzone is 'difficult to define empirically because judgement may vary as to how many and which of the selected diagnostic taxa need be present to identify the zone' (Hedberg 1976, p. 58).

Considered as biostratigraphical units, Oppelzones possess several distinctive features (Sigal 1984; Pignatti 1998). They are (1) part of an ideal succession of superposed key faunas, representing an ideal reference; (2) a zonation based upon Oppelzones is a discrete zonation, that is, adjacent biozones are separated by intervals of unspecified length; (3) not formally defined by their base, being discrete, non-overlapping concurrent-range zones defined upon the loose co-occurrence of an assemblage of taxa; and (4) they may include correlative vicariant taxa present in other regions, where the index taxa of the original key faunas are absent. Basically, all shallow-water fossil zonations are discrete and Oppelian in essence, because of the fossil record along continental margins, where sea level change and depositional patterns produce a discontinuous record, thus preventing the recognition of reliable first and last occurrences.

In the second edition of the ISG (Salvador 1994) and its abridged version (Murphy & Salvador 1999), the Oppelzone was discarded because it was considered 'not (...) to correspond consistently to any one kind of biozone' (p. 63), or not even mentioned. Similarly, both the North American Stratigraphic Code (2005) and the Stratigraphic Code of Russia (Zhamoida 2006) do not mention the Oppelzone among biostratigraphical units (which they treat

summarily), although it would appear to fit within their concept of assemblage biozone. There are only few national codes or guides in which the Oppelzone is mentioned as one of the kinds of biozones, for example in Norway (Nystuen 1989), where it is synonymized with concurrent-range zone. The explicit use of Oppelzones as biostratigraphical units, as employed in Mesozoic ammonite stratigraphy and in Cenozoic larger foraminiferal zonation, is uncommon in other taxonomic groups. Exceptions include occasional examples in spores (Streel *et al.* 1987), radiolarians (Guex *et al.* 2015) and conodonts (Paull 1983); among vertebrates, the Land Mammal ‘Ages’ are conceptually Oppelzones, as explicitly stated by Walsh (1998). There are several reasons why the use of Oppelzones is so rare. (1) Their boundaries are undefined; as they are defined by their characteristic assemblages and not by their lower and upper limits, they are intrinsically more subjective and less appealing than continuous zonations especially in high-resolution biostratigraphy. (2) The distinction between assemblage zones, concurrent-range zones and Oppelzones has been often considered tenuous (Johnson 1979) or non-existent. Often, the Oppelzone has been considered as subcategory of the assemblage zone or the term assemblage zone has been used in its place, a circumstance which we consider rather unfortunate in the light of the clear definition of this kind of zone in Hedberg (1976). (3) Their recognition is rarely provided for in recent stratigraphical codes and guides, upon which most biostratigraphers rely, and this may actually have inhibited their use. (4) Oppelzones are used in groups that are taxonomically diverse, with many genera and species (ammonites) or species-rank taxa (larger foraminifera).

In recent years, however, there have been some advocates for the reintroduction of Oppelzones as biostratigraphic units (Pignatti 1998; Walsh 1998, 2000; McGowran 2005; Carter 2007), or as biochrons (Walsh 1998).

As to the alternative view, that is the Oppelzone as a chronostratigraphical unit, in our opinion, it is necessary to refer to the use of the term zone in Oppel’s (1856–1858) work. Although there, and in his other works (for a summary, see Schweigert 2005), there is no detailed definition of what he intended as a zone, from his use of the concept it seems clear to us that it conforms to the modern definition of chronostratigraphical zone, representing rocks deposited during an interval of time. The Oppelian rationale requires an ideal profile, that is superposed key localities forming an ideal succession (‘Nachdem ich die Reihenfolge der einzelnen Horizonte zusammengestellt und somit das ideale Profil

gefertigt hatte...’; Oppel 1856, p. 4), and key assemblages (characterized by ‘the constant and exclusive occurrence of certain species’, including long-distance vicariant taxa), representing a scale of discrete, non-overlapping time intervals. Another point stressed by Oppel, in analogy with many later biostratigraphers, is the necessity of precise species circumscription for zonal stratigraphy: ‘Je schärfer die Species getrennt ist, desto genauer können auch die Schichten eingetheilt werden.’ (p. 3, Vorrede). He also stated that a zone includes only species that do not occur in any other zone (‘Jeder der einzelnen Zonen sind immer diejenigen Arten beigeschrieben, welche sie besonders charakterisieren und noch in keiner anderen Schichte gefunden wurden.’ p. 15).

Shortly before the publication of Oppel’s monograph, the Jurassic stages were systematized by d’Orbigny (1850), although, contrary to common belief, the majority of the eleven currently accepted stages were not introduced by him, that is the Pliensbachian and Tithonian (introduced by Oppel himself in 1856), Hettangian, Aalenian, Bathonian, Oxfordian and Kimmeridgian (see Ogg & Hinnov 2012). Not surprisingly, these stages share a common feature: most of them are intimately linked to ammonites.

Oppel’s approach was a top-down approach, starting from the construction of an ‘ideal profile’, an ideal succession of 33 key faunal assemblages for the Jurassic, each representing a zone (Oppel 1858, p. 822–823, Table 63). In naming his zones, among index fossils ammonites prevailed, but one-third was based on other taxa, such as brachiopods, bivalves, gastropods, crinoids and echinoids. In this famous table (reproduced in Arkell 1933, table 3), zones are characterized as ‘Lager oder Stufen, d. h. paläontol. bestimmbare Schichtencomplexe’ (‘layers or stages, i.e., palaeontologically determinable complexes of strata’; our translation and emphasis). However, in the same table stages (*Etagen*) are defined as synonymous with ‘groups of zones’ (*Zonengruppen*), thus leading many stratigraphers to the interpretation that his zones are chronostratigraphical units.

Walsh (1998) provided a complex theoretical clarification of the two distinct meanings of Oppelzones, biostratigraphical (‘Oppel fossilzone’) and biochronological (‘Oppel biochron’), and within the units, he, respectively, termed ‘assemblage interval fossilzones’ and ‘assemblage interval biochrons’. In order to avoid needless proliferation of names, later Walsh (2000) retracted the term ‘fossilzone’, reverting to its much more used synonym ‘biozone’, or simply ‘zone’. Within each kind of unit, he distinguished three subcategories: disjunctive zone, minimal overlap zone and strict overlap zone. In our

1 opinion, however, the precise recognition of these
2 different subcategories introduced by Walsh (1998)
3 in biostratigraphy and biochronology, although the-
4oretically sound, appears hardly feasible in practice.

6 Ammonoids and larger foraminifera: 7 a parallel history of biozonation

8 Shifting the perspective from theory to practice, it
9 seems appropriate to examine briefly how
10 ammonitologists and foraminiferologists have dealt
11 with this issue. Our aim here is not a comprehen-
12sive review of the history of biozonation in Jurassic
13 ammonites and Palaeogene–Neogene larger forami-
14nifera. Instead, we wish to summarize the rationale
15 of the present approaches to biozonation in these
16 groups, pointing out similarities and differences,
17 and keeping the historical development in these
18 two fields to a minimum, as the vast literature on
19 Jurassic ammonite biozonation cannot be dealt
20 with in detail here. In Western European Jurassic
21 ammonoid stratigraphy (e.g. Callomon 1994, 1995;
22 Corna *et al.* 1997), the term Oppelzone – as dis-
23tinct from Hedberg’s (1976) biostratigraphic
24 Oppel-zone – has been generally regarded to coin-
25cide with chronozone and standard zone (Meister
26 2010). Similarly, in Russia, at least since Stepanov
27 (1958) introduced this concept, Oppelzones were
28 generally accepted as chronostratigraphical units
29 (Gladenkov 2010).

30 The Oppelian ammonite chronostratigraphy rep-
31resents a primary standard, necessary for hierarchical
32 consistency, directly tied with the definition of Juras-
33sic-Cretaceous stages and their GSSPs, in spite of the
34 uncertainties in correlation among regional (do-
35main, realm) ammonite zonations. As chronostrati-
36graphical units, these ammonite Oppelzones
37 (chronozones and standard zones): (1) are formally
38 defined at their base; (2) reflect a continuous zonation;
39 and (3) are related hierarchically: chronozone
40 or (standard) zone, subchronozone or (standard)
41 subzone, and ‘zonule’ (sensu Hedberg 1976). In each
42 major faunal realm or province (boreal, subboreal,
43 sub-Mediterranean, Mediterranean, etc.), the Juras-
44sic is currently subdivided into 70–80 standard zones
45 and 160–170 subzones (Ogg & Hinnov 2012).

46 In contrast to ammonite chronostratigraphy,
47 ammonite biostratigraphy (Kennedy & Cobban
48 1977) is based on biohorizons (also called simply
49 ‘horizons’; Page 1995), which are the least inclusive
50 and fundamental unit in a hierarchy of biozones
51 (Page 2003; Meister 2010; Rogov *et al.* 2012). Bio-
52 horizons are biozones that correspond to a bed or a
53 series of beds, characterized by one or more taxa,

within which no further subdivision can be made, at
least on a local basis (Gabilly 1976). Individual bio-
horizons are generally confined to one to few palaeo-
geographical regions.

The number of ammonite biohorizons largely
exceeds that of corresponding zones and subzones.
For example, in the Jurassic of France about 68
zones, 160 subzones and 292 biohorizons are distin-
guished in Cariou & Hantzpergue (1997). Assuming
a duration of the Jurassic of 56.3 myr as in the
GTS2012 (Ogg & Hinnov 2012), in the French Juras-
sic, the average time span of a zone would corre-
spond to ca. 828 kyr, of a subzone 352 kyr and of a
biohorizon 193 kyr. However, such an inference of
average duration is misleading for biohorizons, by
definition. At a local or regional scale, a biohorizon,
however defined, is a discrete unit, separated by hia-
tuses of unknown duration from other adjacent bio-
horizons and a scale of biohorizons consequently
represents a discrete zonation. Degrees of increasing
inclusiveness characterize, respectively, the biohori-
zon, the faunal horizon and the standard horizon; at
regional scale, in addition the concept of ‘biosub-
zone’ (or simply ‘biozone’) has been used (Meister
2010). In contrast to ammonite standard zones
(chronozones, Oppelzones), these biozones may
conform to any different zonal criteria, such as total
range zone, acme-zone, partial range zone, assem-
blage zone, phylozone, interval zone, including the
Oppelzone sensu Hedberg (1976). The recognition
of biohorizons, that is of clearly distinct, superposed
fossil assemblages, is like building up a ladder step
by step. Regardless of the empty spaces between one
and the successive step, it covers entirely the vertical
space between its base and its top. To provide a clar-
ification of these concepts, a diagrammatic model is
set out in Figure 1.

Although the temporal acuity obtained through
ammonites is unparalleled by any other fossil group
used in Jurassic biostratigraphy, a cautionary note is
appropriate (Zeiss 2003). First, long-range biohori-
zon correlation is not straightforward, because each
major palaeogeographical unit has its own parallel
zonation or zonations of biohorizons; often, addi-
tional elements (e.g. magnetostratigraphy, microfossils)
are needed to achieve correlation. Second, the
index-species of some horizons may be rare (Dom-
mergues *et al.* 1997), thus hampering their recogniz-
ability. An example is *Beaniceras luridum* (Simpson)
in NW Europe, the index-species of the Luridum
horizon (Dean *et al.* 1961), Luridum Subzone,
within the IbeX Zone (Pliensbachian), a zone estab-
lished by Oppel (1856).

As chronostratigraphical units, Oppelzones may
be considered as an historical necessity, because they

1 represent an embryo of a time-scale. As stated by
2 Callomon (1994, p. 22), 'conceptually, (...) Oppel's
3 Zones were mer[e]ly thinner slices of the standard
4 geological column'.

5 It is now interesting to compare the history and
6 rationale of biozonation in ammonoids with that in
7 larger foraminifera (also known as larger benthic
8 foraminifera). When Oppel's *Juraformation*
9 appeared, a rudimentary zonation for Eocene-Oligo-
10 cene nummulitids already existed (d'Archiac 1850;
11 d'Archiac & Haime 1853). Later, a number of
12 authors, such as de la Harpe, Boussac, Prever, and
13 H. and R. Douvillé, proposed various regional scales
14 based on larger foraminifera that today have mainly
15 historical interest. These zonations focused mainly
16 on the Eocene and Oligocene of France, Switzerland,
17 Italy and other circum-Mediterranean countries;
18 they were more top-down (i.e. reflecting the ideal
19 vertical sequence of stages, formations and fossilifer-
20 ous key localities) than bottom-up (i.e. established
21 through the detailed analysis of fossiliferous succes-
22 sions). Generally, in these scales larger foraminifera,
23 along with macrofossils, were used as *Leitfossilien*
24 (index fossils) for particular stratigraphical intervals
25 (mostly at stage or substage level), through the
26 superposition of key species from different regions,
27 rather than as zonal markers in a modern sense. In
28 addition, some of these early attempts were affected
29 in part by the non-recognition of reworking.

30 Not surprisingly, in larger foraminifera the turn-
31 ing point from coarse to fine-scaled zonation coin-
32 cided with conspicuous advances on two distinct
33 fronts. As to the first front, the systematics and phy-
34 logeny of the taxa used in biozonation needed to be
35 adequate; as in other fossil groups, zonation lagged
36 behind major systematic advances. Systematics in
37 larger foraminifera basically follows two different
38 approaches (typological vs. biometrical) (Pignatti
39 1998).

40 In the typological approach (Hottinger 2013),
41 species are defined and identified by reference to a
42 type, a specimen that is a term of comparison in
43 respect to other types (ideally, two at a time), each
44 presenting distinctive characters. Emphasis is not on
45 the biometrical characterization of populations, but
46 on their comparison with other coeval taxa, or
47 stratigraphically superposed phylogenetically related
48 taxa. As visual comparison is deemed particularly
49 important, illustration of taxa is standardized and
50 profuse (Hottinger 1960; Schaub 1981). For biozonal
51 assignment, usually the whole assemblage of co-
52 occurring taxa is taken into account. Multiple coeval
53 biozones are established on distinctive successive
54 species from parallel, well-known lineages (Schaub
55 1981) of different genera (*Alveolina*, *Nummulites*,

Assilina), originating from stratigraphically super-
posed key localities, and correlated to each other
(Hottinger *et al.* 1964). The ensuing zonation is dis-
crete (Guex *et al.* 2015) and Oppelian in Hedberg's
(1976) meaning.

6 In the biometrical approach (Drooger 1993; Less
& Ó. Kovács 2009), species and subspecies, consid-
7 ered as lineages formed of semi-statistical popula-
8 tions, are defined as morphometrical units. Lineages
9 showing a morphometrical continuum are subdiv-
10 ided into arbitrary segments, representing chrono-
11 (sub)species; the ensuing biozonations are either
12 phylozones (lineage-zones sensu Hedberg 1976) or
13 mixed, with phylozones and interval zones (e.g.
14 Drooger & Laagland 1986; Laagland 1990; Drooger
15 1993), or phylozones, interval zones and Oppel-
16 zones sensu Hedberg (1976) (e.g. Less 1998) when in
17 addition to morphometric boundaries, first or last
18 occurrences of genera or species are used as data to
19 produce a continuous zonation (Guex *et al.* 2015).

20 These separate biozonation approaches reflect
21 thus different: (1) species concepts and identification
22 methods (typological vs. biometrical; Pignatti 1998),
23 resulting in different kinds of biozones (mainly,
24 Oppelzones sensu Hedberg and phylozones); (2)
25 palaeoecological constraints: all groups of larger for-
26 aminifera are ecologically restricted taxa (Hottinger
27 1997), hence the necessity to establish multiple bio-
28 zonations for a same biogeographical region (Fig. 2);
29 and (3) stratigraphical ranges of individual single-
30 taxon biozonations, that is the vertical range of each
31 taxonomic group used for biozonal stratigraphy
32 (Fig. 2).

33 Two important analogies between the discrete and
34 continuous larger foraminiferal zonations need to be
35 pointed out. First, none of the single-taxon zonation
36 employs abundance criteria, such as acme
(Hedberg 1976), LCO (last common occurrence),
37 for the definition of zonal boundaries. Second, both
38 the typological and the biometrical methods have
39 deal with the issue of populations that are transi-
40 tional between two subsequent taxa or morphomet-
41 ric subdivisions of a lineage, for which the
42 typological approach uses terms such as 'transitional
43 form' or 'aff.' (Schaub 1981), whereas the biomet-
44 rical approach employs the term *exemplum inter-*
45 *centrale* (Drooger 1993).

46 As to the second front, it was necessary to achieve
47 sufficient sampling detail along representative fossil-
48 iferous successions and to construct range charts
49 that could be compared from different depositional
50 facies and regions. In the course of the 20th century,
51 in contrast to planktonic microfossil studies, which
52 were largely dependent from ocean drilling projects,
53 larger foraminiferal zonations were strongly linked

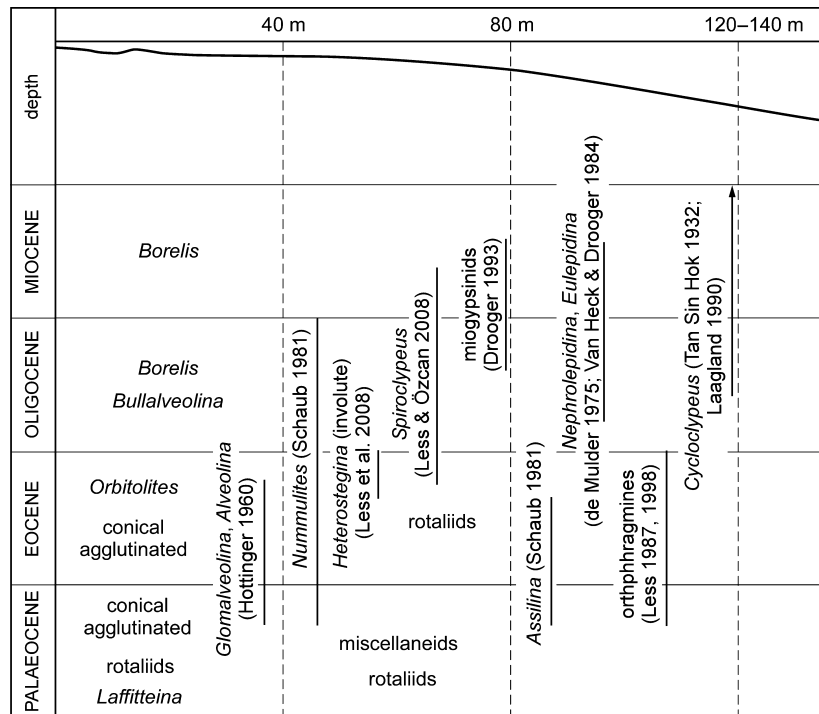


Fig. 2. Inferred distribution along the depth gradient of selected groups of Palaeocene–Miocene larger foraminifera on which single-taxon biozonations have been established; depth ranges of taxa are simplified after Hottinger (1997) and may actually overlap.

with the unprecedented expansion of field geology and, at least regionally, oil industry (e.g. in the Middle East and SE Asia).

Thus, at the end of the 1920s, a distinct larger foraminiferal biozonation, the ‘Letter Classification’ (also known as ‘Letter Stages’), was first proposed by van der Vlerk & Umbgrove (1927) for the East Indian Tertiary (now mainly Indonesia). It was based on assemblage biozones of genera and species of larger foraminifera and recognized in the Palaeogene–Neogene six main zones, labelled ‘a’ through ‘f’ (e.g. Tertiary ‘a’ or ‘Ta’). These biozones were practical tools of Tertiary stratigraphy in SE Asia, a replacement for the apparently ‘unreliable and unwieldy European epochs’ and stages (Lunt 2013). The SE Asian Letter ‘stages’ had no type sections; much later, Adams (1970) attempted to give the Letter Stages a more objective stratigraphical basis, redefining the ranges of their markers, introducing subdivisions (such as Ta1, Ta2) and extending it from Iran to the Western Pacific and Australia. Later, this zonation was further extended, for example to the Philippines and Japan, refined and correlated with planktonic foraminiferal zones (BouDagher-Fadel & Banner 1999; BouDagher-Fadel 2002, 2008).

In the same region, soon both van der Vlerk (e.g. 1955; and references therein) and especially Hok

(1932) were pioneers in the biometric investigation of larger foraminiferal lineages for systematic and biostratigraphical purposes. Using *Cycloclypeus*, Hok (1932, p. 127) first proposed 12 biometry-based lineage zones (i.e. phylozones) from the Oligocene to the Plio–Pleistocene, and introduced the term ‘nepionic aurora’ or simply ‘aurora’ for the chronologic interval corresponding to a chrono(sub)species. Since the 1950s, this line of investigation has been successfully developed – especially by the ‘Utrecht School’ – in radial foraminifera (e.g. De Mulder 1975; Drooger & Laagland 1986; Drooger 1993), orthophragmines (Less 1987) and nummulitids (*Cycloclypeus*: Laagland 1990; *Heterostegina*: Less et al. 2008; *Spiroclypeus*: Less & Özcan 2008). In these groups, zonations are mainly either phylozones (lineage zones) or a combination of phylozones based on biometrically defined chrono(sub)species and interval zones (Fig. 3). The orthophragmine zonation (Less 1987, 1998; Less et al. 2007) is a special case, in which Opperl-zones and phylozones are combined. The biometrical definition of chrono(sub)species as arbitrarily but objectively defined segments of lineages produces a continuous zonation (Guex et al. 2015).

More or less at the same time when the ‘Utrecht School’ started, the breakthrough for establishing an Eocene nummulitid zonation was Schaub’s (1951)

monograph on *Nummulites* and *Assilina* from flysch formations of Switzerland, a meticulous bottom-up study unravelling the main lineages through typological methods. Through Hottinger's (1960) study of alveolinids, an integrated parallel scale of nummulitid and alveolinid biozones for the circum-Mediterranean area was established, first presented in 1962 at the Colloquium on the Palaeogene in Bordeaux (Hottinger *et al.* 1964). This zonation and unparalleled systematic results (Schaub 1981) represent a seminal contribution of the 'Basle school' in larger foraminifera (Hottinger 2013). These biozones based on nummulitids and alveolinids followed the Oppelian criteria of superposed key localities, key assemblages and vicariant taxa and thus represented a discrete biozonation. The faunal succession and the association of its elements permitted parallel correlation of biozones based on ecologically different groups (e.g. alveolinids, *Nummulites* and *Assilina*). In addition, species circumscription was typological. Given that Oppelzones are intrinsically prone to

correlation, their correlation with biozonations established on different taxonomic groups started quite early; for example, nummulitid biozones were correlated with the calcareous nannoplankton (Kapellos & Schaub 1973) and planktonic foraminiferal zones (e.g. von Hillebrandt 1975).

Since Serra-Kiel *et al.* (1998), this classical paradigm has been superseded for the Palaeocene and Eocene by twenty SBZ (or SB) biochronozones, at least in part correlated to magnetostratigraphy, mainly based on the Pyrenean domain. At the same time, Cahuzac & Poignant (1997) extended this scale to the Oligocene and Miocene (SB 21–SB 26), mainly basing on Western France. The SB zonation combines the biostratigraphic zonations based on alveolinids (Hottinger 1960), *Nummulites* and *Assilina* (Schaub 1981), orthophragmines (Less 1987, 1998), *Heterostegina*, lepidocyclinids, *Cycloclypeus* and miogypsinids (Drooger 1993), and other taxonomic groups. This zonation remains largely Oppelian, even if it contains the non-Oppelian lepidocyclinid

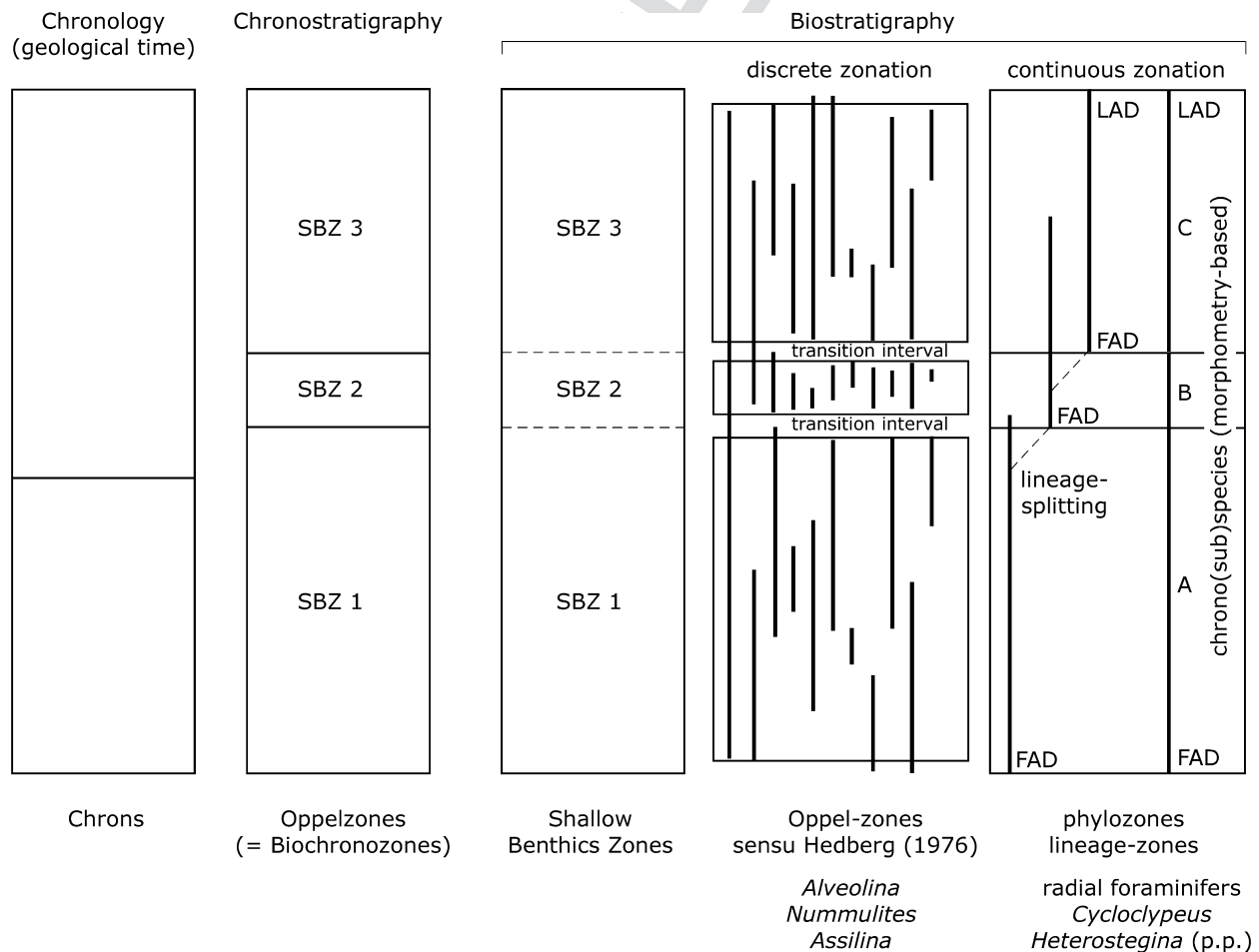


Fig. 3. The Shallow Benthic Zonation (Cahuzac & Poignant 1997; Serra-Kiel *et al.* 1998) in larger foraminiferal biostratigraphy: from Oppel-zones sensu Hedberg (1976) and phylozones to Oppelzones (biochronozones).

1 and miogypsinid zones and the partly Ope-
2 llian orthophragmine zones, because it uses extensively
3 the vicariance of different groups, laterally substitut-
4 ing each other and more or less coeval. Moreover,
5 the SB zonation is linked both to calcareous plank-
6 ton and nannofossil scales and to the magnetostrati-
7 graphical chrons as given in Berggren *et al.* (1995),
8 adding a significant information useful for world-
9 wide correlation and achieving the status of a 'stan-
10 dard' zonation, as shown by its inclusion in the
11 new edition of the Geological Time Scale (Hilgen
12 *et al.* 2012; Vandenberghe *et al.* 2012).

13 Conversely, whereas larger foraminifera were con-
14 spicuously present in the former stratotypes of
15 Palaeogene stages, they are now usually lacking in
16 the type sections the GSSPs, established on deep-
17 water deposits. The main exception is the Lutetian
18 GSSP in Gorrondatxe (Molina *et al.* 2011) for which
19 the SB zones were recognized already in the prelimi-
20 nary studies (Payros *et al.* 2007, 2009).

21 In the last decades, several regional larger forami-
22 niferal zonations were established, for example for
23 Oman (Racey 1994, 1995), the Indian Himalayas
24 (Mathur *et al.* 2009) and Tibet (BouDagher-Fadel
25 *et al.* 2015). In contrast, although the systematics
26 and biometry of various groups of radial forami-
27 nifera from the Americas and the Caribbean have been
28 investigated in detail (Drooger 1993; BouDagher-
29 Fadel & Price 2010a,b), no 'standard' larger forami-
30 niferal zonation is yet available. An attempt (based
31 on unreferenced data) that did not gain general
32 acceptance is that developed for the Mexican oil
33 industry (Butterlin 1981), that uses five biozones
34 subdivided into thirteen sub-biozones (loosely
35 defined assemblage, total and partial range biozones)
36 for the Palaeocene–middle Miocene. A larger forami-
37 niferal zonation for the Palaeogene of Jamaica
38 and the Caribbean area is that by Robinson &
39 Wright (1993).

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44 As discussed above, Opepzones were listed by Hed-
45 berg (1976) in the first edition of the ISG. Even if
46 the definition reported seems to be different from
47 the original concept of zone by Opep, there are
48 some issues deserving further discussion.

49 First, in Hedberg's (1976) definition of an Opep-
50 Zone, vicariance is not explicitly mentioned,
51 although he specifies that 'not all of the taxons con-
52 sidered diagnostic need be present at any one place'
53 and 'supplementary use of biostratigraphical criteria

other than range-concurrence that are thought to be
54 useful in demonstrating time-equivalence' is
55 allowed. Through this omission, one of the main
advantages of the Opepzones is lost, namely the
possibility to use them, through additional taxa, in
different palaeoenvironmental settings with the same
biochronological significance. In the current SB
zonation, which remains essentially Opepian, we
can use the same biozone along the palaeobathymet-
ric gradient.

Second, there are strong analogies between the
Opepzone and the Assemblage zone as defined in
Hedberg (1976). The main difference is that the for-
mer implies 'an association or aggregation of *selected*
taxons [...] chosen as indicative of approximate
contemporaneity', whereas the latter is defined as 'a
body of strata whose content [...] constitutes a *natural*
assemblage' (italics as in the original). In both
cases, the boundaries are fuzzy: '[t]he total range of
any constituent taxon may extend beyond the
boundaries of the assemblage-zone' and '[b]ecause
of the complexity and indefiniteness of Opep-zone
criteria, boundary positions are to a considerable
extent subject to worker's judgement'.

In the subsequent second edition of the ISG by
Salvador (1994), and in the later abridged version
(Murphy & Salvador 1999), the Opepzone has been
deleted and the definition of the assemblage zone is
'a stratum or body of strata characterized by a dis-
tinctive assemblage or association of three or more
fossil taxa that, taken together, distinguishes it in
biostratigraphic character from adjacent strata' (Sal-
vador 1994). A similar concept is presented in the
most recent North American Commission on Strati-
graphic Nomenclature (2005). The inherent fuzzy
definition of the boundaries of the Opepzone is
maintained in the assemblage zone representing at
the same time a weakness (because of subjectivity in
determining them) and a main advantage (because
of their flexibility in being applied to different
palaeoenvironmental settings).

Scott (2013) claims that the definition of Opep-
zone in Hedberg (1976) is ambiguous, suggesting
that this 'equivocal status' could be the reason for its
removal in the revised ISG by Salvador (1994). Any-
way, the problem remains for the assemblage zone,
which seems to be some new name for the same
Opepian conception.

56 Conclusions

An advantage of Opepzones is that they help
addressing zonal recognition and correlation

difficulties arising from two constraints: (1) *palaeoenvironmental constraint*: by integrating biozonations based on different taxa according the depth gradient. The genera and lineages used for establishing biozonations are linked and depend on specific conditions along the depth gradient; and (2) *palaeobiogeographic constraint*: using vicariant taxa, there is no need that a given taxon must be present in all places. Because of (1), Oppelzones allow also the establishment of local zonations and their integration, just as in Jurassic ammonites.

On the other hand, the unparalleled biostratigraphic potential of ammonites resides in the huge number of their basic units, the biohorizons. Their numbers cannot be achieved in larger foraminifera. However, there is latitude for exploring further subdivisions of biozonal units in larger foraminifera, such as using: (1) subtle variations in morphology, as characterized through biometrical studies, or (2) prominent variations in abundance of selected taxa linked to variations in the physical environment, producing at regional to global scale, such as those linked to major eustatic events or strong changes in sea surface temperature fluctuations (PETM, MECO, etc.).

As discussed above, both in Jurassic ammonite and Cenozoic larger foraminiferal stratigraphy, Oppelzones have been used as biostratigraphical and chronostratigraphical tools. In the Shallow Benthic Zonation (Cahuzac & Poignant 1997; Serra-Kiel *et al.* 1998; BouDagher-Fadel *et al.* 2010c), the parallel single-taxon biozonations were merged to build a scale that attempts to be a 'standard' system of biochronozones. In contrast to other micro-fossil zonations, these biochronozones are mostly neither linked to biostratigraphic events such as FOs and HOs and their correlative FADs and LADs, nor to abundance criteria: with a few exceptions, they rely on the concurrent occurrence of several taxa of independent lineages. Intrinsicly thus, the recognition of the boundaries between zones is somewhat subjective. Therefore, correlating larger foraminiferal biozones with other biozonal scales, magnetostratigraphy, isotope stratigraphy, etc., to achieve a complete and reliable system of biochronozones needs at least some additional criteria reducing subjectivity, that have indeed been implemented over the years (Papazzoni *et al.* 2017).

Firstly, since the 1960s, when the foundations of a stable system of parallel single-taxon zonations were established, there has been a conspicuous refinement of systematics in many additional larger foraminiferal groups, such as the rotaliids, the conical agglutinated and the porcelaneous forms. These taxa and

their bio-events may be used as further biostratigraphical constraints.

Secondly, in the last decades, several previously understudied intervals, such as the Palaeocene, and geographical areas (Asia, Central America and the Caribbean) have yielded an amount of new systematic and distributional data, providing many additional potential biostratigraphical markers. Whereas at species level the vertical ranges of these taxa are still incompletely known, the elements which have the highest potential of becoming useful standard markers are those linked to first and last occurrence of genera. There is not only a potential for more accurate correlation, but also for zonal identification, as the recognition of genera is rather straightforward in larger foraminifera because of their complex shells: genera are distinguished by qualitative characters, species by quantitative characters.

Thirdly, starting with the seminal study by Hok (1932), who first used biometrical methods to investigate evolutionary change through time within lineages of *Cycloclypeus* and suggest a biozonation based on successive morphometrical populations, since the 1980s there are several useful zonal scales based on morphometric criteria that still need to be tested more extensively, but may provide additional objective biostratigraphical data for large-scale correlation. In addition, biometrical methods may provide the means for further refinement of the SB zonation: using successive Bartonian–Priabonian chronosubspecies of *Heterostegina*, Less *et al.* (2008) proposed to subdivide SBZ 18 into three subzones and SBZ 19 into two. We maintain that the main reason for this insufficient knowledge is the lack of interest for biometrical methods in biostratigraphy among many palaeontologists (Dzik 1994), also because the involved splitting, sectioning and measuring work is considered as time-consuming.

Finally, we suggest that the Shallow Benthic Zonation and the regional larger foraminiferal zonations established in different palaeobiogeographical domains (Mediterranean Neotethys, Oman–Iran, Indian Himalaya, Tibet, SE Asia) should be conceived as, respectively, corresponding to the (Oppe- lian) ammonite chronozones (standard zones) and the regional (domain, realm) ammonite zonations. Different kinds of biozones (Oppel zones sensu Hedberg, phylozones, mixed zonations) are subsumed under the biochronostratigraphic SBZ system in a similar way as regional ammonite zonations are integrated in the standard ammonite zonation. Correlation of the SB zonation with global events is not straightforward. In some cases, however, as for the Palaeocene/Eocene boundary, which is defined by an isotopic shift of C and O, the global signal is

detectable in shallow-water settings, too, allowing direct correlation (Scheibner & Speijer 2009; Zhang *et al.* 2013). Among the more recent attempts of direct correlation of the SBZ with calcareous plankton, nannofossils and magnetostratigraphy, there are works from Spain (e.g. Rodríguez-Pintó *et al.* 2012; Costa *et al.* 2013) and Italy (Papazzoni *et al.* 2014).

In conclusion, the Achilles' heel of Opeelian zonation hinges on a paradox. In both Jurassic ammonites and Tertiary larger foraminifera, a striking feature is that their fossil record and many biostratigraphical units based upon them (biohorizons, Opeelzones) are discontinuous, and thus, the resulting biozonations are discrete (Guex *et al.* 2015). However, in both groups, 'standard' (bio)chronostratigraphical scales are, by definition, continuous. The solution of this apparent paradox hinges on the analytical methods used to correlate biostratigraphical and chronostratigraphical units. To achieve correlation, (bio)chronostratigraphical units should be based on as few as possible markers, and not assemblages of taxa, as in biostratigraphical Opeelzones. This implies that, in contrast to Serra-Kiel *et al.* (1998), the number of taxa used to define the SB biochronozones should be reduced to single taxa and their correlative data. Conversely, Opeelian larger foraminiferal biozones should maintain their polytaxic definition, to permit recognition in sediments from different environments and regions; both single-taxon and regional zonation should coexist with these Opeelzones. Thus, a novel research programme is needed to (1) establish the most suitable markers for biozonal boundaries; (2) enhance correlation with different systematic groups (especially planktonic foraminifera and calcareous nannofossils) and with other stratigraphical tools (magnetostratigraphy, radiometric dating, isotopic stratigraphy, etc.); and (3) extend morphometric criteria wherever possible to recognize the markers themselves.

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References

- Adams, C.G. 1970: A reconsideration of the East Indian Letter Classification of the Tertiary. *Bulletin of the British Museum (Natural History)*, *Geology* 19, 87–137.
- d'Archiac, A. 1850: *Histoire des progrès de la géologie de 1834 à 1849; Première partie, volume 3*, 1–624. Société géologique de France, Paris.
- d'Archiac, A. & Haime, J. 1853: *Description des animaux fossiles du groupe nummulitique de l'Inde, précédée d'un résumé géologique et d'une monographie des Nummulites*, 373 pp. Gide et Baudry, Paris.
- Arkell, W.J. 1933: *The Jurassic System in Great Britain*, 681 pp. Oxford University Press, Oxford.
- Arkell, W.J. 1956: *Jurassic Geology of the World*, 806 pp. Oliver and Boyd, Edinburgh.
- Balini, M., Ferretti, A., Finney, S. & Monechi, S. 2017: The contribution of fossils to chronostratigraphy, 150 years after Albert Opeel. *Lethaia* ???, ???–??? (this issue).
- Berggren, W.A., Kent, D.V., Swisher, C.C. & Aubry, M.-P. 1995: A revised Cenozoic geochronology and chronostratigraphy. In Berggren, W.A., Kent, D.V., Aubry, M.-P. & Hardenbol, J. (eds): *Geochronology, Time Scale and Global Correlations: An Unified Temporal Framework for an Historical Geology. SEPM, Special Publications* 54, 129–212.
- BouDagher-Fadel, M.K. 2002: The stratigraphical relationship between planktonic and larger benthic foraminifera in Middle Miocene to Lower Pliocene carbonate facies of Sulawesi, Indonesia. *Micropaleontology* 48, 153–176.
- BouDagher-Fadel, M.K. 2008: *Evolution and Geological Significance of Larger Benthic Foraminifera*, 540 pp. *Developments in Palaeontology and Stratigraphy* 21. Elsevier, Amsterdam.
- BouDagher-Fadel, M.K. & Banner, F.T. 1999: Revision of the stratigraphic significance of the Oligocene-Miocene 'Letter-Stages'. *Revue de Micropaléontologie* 42, 93–97.
- BouDagher-Fadel, M.K. & Price, G.D. 2010a: Evolution and paleogeographic distribution of the lepidocyclinids. *Journal of Foraminiferal Research* 40, 79–108.
- BouDagher-Fadel, M.K. & Price, G.D. 2010b: American Mio-gypsinidae: an analysis of their phylogeny and biostratigraphy. *Micropaleontology* 56, 567–586.
- BouDagher-Fadel, M.K., Price, G.D. & Koutsoukos, E.A.M. 2010c: Foraminiferal biostratigraphy and paleoenvironments of the Oligocene-Miocene carbonate succession in Campos Basin, southeastern Brazil. *Stratigraphy* 7, 283–299.
- BouDagher-Fadel, M.K., Price, G.D., Hu, X. & Li, J. 2015: Late Cretaceous to early Paleogene foraminiferal biozones in the Tibetan Himalayas, and a pan-Tethyan foraminiferal correlation scheme. *Stratigraphy* 12, 67–91.
- Butterlin, J. 1981: *Claves para la determinación de macroforaminíferos de México y del Caribe, del Cretácico superior al Mioceno medio*, 219 pp. Publicaciones del Instituto Mexicano del Petróleo, México.
- Cahuzac, B. & Poignant, A. 1997: Essai de biozotation de l'Oligo-Miocène dans les bassins européens à l'aide des grands foraminifères néritiques. *Bulletin de la Société géologique de France* 168, 155–169.
- Callomon, J.H. 1994: Palaeontological methods of stratigraphy and biochronology: some introductory remarks. *Geobios, Mémoire Speciale* 17, 16–30.
- Callomon, J.H. 1995: Time from fossils: S.S. Buckman and Jurassic high-resolution geochronology. In Le Bas, M.J. (ed.): *Milestones in Geology. Memoirs of the Geological Society of London* 16, 127–150.
- Cariou, E. & Hantzpergue, P. (eds) 1997: (Groupe Français d'Etude du Jurassique) Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonation parallèles et distribution des invertébrés et microfossiles. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine, Mémoire* 17, 1–422.
- Carter, R.M. 2007: Stratigraphy into the 21st century. *Stratigraphy* 4, 187–193.
- Corna, M., Dommergues, J.-L., Meister, C. & Page, K. 1997: Les faunes d'ammonites du Jurassique inférieur (Hettangien, Sinémurien et Pliensbachien) au nord du massif des Écrins (Oisans, Alpes occidentales françaises). *Revue de Paléobiologie* 16, 321–409.
- Costa, E., Garcés, M., López-Blanco, M., Serra-Kiel, J., Bernaola, G., Cabrera, L. & Beamud, E. 2013: The Bartonian-Priabonian marine record of the eastern South Pyrenean foreland basin (NE Spain): a new calibration of the larger foraminifera and

- calcareous nannofossil biozonation. *Geologica Acta* 11, 177–193.
- De Mulder, E.F.J. 1975: Microfauna and sedimentary-tectonic history of the Oligo-Miocene of the Ionian Islands and western Epirus (Greece). *Utrecht Micropaleontological Bulletins* 13, 1–140.
- Dean, W.T., Donovan, D.T. & Howarth, M.K. 1961: The Liassic ammonite zones and subzones of the north west European Province. *Bulletin of the British Museum (Natural History) Geology* 4, 435–505.
- Dommergues, J.-L., Meister, C. & Mouterde, R. 1997: Pliensbachien. In Cariou, E. & Hantzpergue, P. (eds): *Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine, Mémoire* 17, 15–23.
- Drooger, C.W. 1993: Radial Foraminifera; morphometrics and evolution. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde* 41, 1–242.
- Drooger, C.W. & Laagland, H. 1986: Larger foraminiferal zonation of the European-Mediterranean Oligocene. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen (B)* 89, 135–148.
- Drooger, C.W. & Rohling, E.J. 1998: *Lepidocyclina* migration across the Atlantic. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen (B)* 91, 39–52.
- Dzik, J. 1994: Range-based biostratigraphy and evolutionary geochronology. In *Proceedings of the 3rd Pergola International Symposium. Palaeopelagos Special Publication* 1, 121–128.
- Gabilly, J. 1976: *Le Toarcien à Thouars et dans le Centre-Ouest de la France*, 217 pp. Comité Français de Stratigraphie, 3. C.N.R.S., Paris.
- Gladenkov, Y. 2010: Zonal biostratigraphy in the solution of the fundamental and applied problems of geology. *Stratigraphy and Geological Correlation* 18, 660–673.
- Guex, J., Galster, F. & Hammer, Ø. 2015: *Discrete Biochronological Time Scales*, 160 pp. Springer, Cham.
- Hancock, J.M. 1977: The historic development of biostratigraphic correlation. In Kauffman, E.G. & Hazel, J.E. (eds): *Concepts and Methods of Biostratigraphy*, 3–22. Dowden, Hutchinson & Ross, Stroudsburg.
- Hedberg, H.D. 1976: *International Stratigraphic Guide*, 200 pp. Wiley, New York.
- Hilgen, F.J., Lourens, L.J. & Van Dam, J.A. 2012: The neogene period. In Gradstein, F.M., Ogg, J.G., Smith, A.G. & Ogg, G.M. (eds): *The Geologic Time Scale 2012*, 923–978. Elsevier, Amsterdam.
- von Hillebrandt, A. 1975: Corrélation entre les biozones de grands foraminifères et de foraminifères planctoniques de l'Ilerdien. *Bulletin de la Société géologique de France* 17, 162–167.
- Hok, T.S. 1932: On the genus *Cycloclpeus* Carpenter. Part I, and an appendix on the *Heterostegines* of Tjimanggoe, S. Bantam, Java. *Wetenschappelijke Mededeelingen Dienst van den Mijnbouw in Nederlandsch-Indië* 19, 1–194.
- Hottinger, L. 1960: Recherches sur les alvéolines du Paléocène et de l'Éocène. *Schweizerische Paläontologische Abhandlungen* 75–76, 1–243.
- Hottinger, L. 1997: Shallow benthic foraminiferal assemblages as signals for depth of their deposition and their limitations. *Bulletin de la Société géologique de France* 168, 491–505.
- Hottinger, L. 2013: Micropalaeontology in Basel (Switzerland) during the twentieth century: the rise and fall of one of the smaller fields of the life sciences. In Bowden, A.J., Gregory, F.J. & Henderson, A.S. (eds): *Landmarks in Foraminiferal Micropalaeontology: History and Development*, 317–335. Micropalaeontological Society, Special Publications, London.
- Hottinger, L., Lehmann, R. & Schaub, H. 1964: Données actuelles sur la biostratigraphie du Nummulitique méditerranéen. *Mémoire du Bureau de Recherches Géologiques et Minières* 28, 611–652.
- Johnson, J.G. 1979: Intent and reality in biostratigraphic zonation. *Journal of Paleontology* 53, 931–942.
- Kapellos, C.C. & Schaub, H. 1973: Zur Korrelation von Biozonierungen mit Grossforaminiferen und Nannoplankton im Paläogen der Pyrenäen. *Eclogae Geologicae Helvetiae* 66, 687–737.
- Kennedy, W.J. & Cobban, W.A. 1977: The role of ammonites in biostratigraphy. In Kauffman, E.G. & Hazel, J.E. (eds): *Concepts and Methods of Biostratigraphy*, 309–320. Dowden, Hutchinson & Ross Inc., Stroudsburg.
- Laagland, H. 1990: *Cycloclpeus* in the Mediterranean Oligocene. *Utrecht Micropaleontological Bulletins* 39, 1–171.
- Less, G. 1987: Paleontology and stratigraphy of the European Orthophragminae. *Geologica Hungarica, Series Palaeontologica* 51, 1–373.
- Less, G. 1998: The zonation of the Mediterranean Upper Paleocene and Eocene by Orthophragminae. *Dela, Slovenska akademija znanosti in umetnosti, Opera, Academia Scientiarum et Artium Slovenica* 34, 21–43.
- Less, G. & Ö. Kovács, L. 2009: Typological versus morphometric separation of orthophragminid species in single samples – a case study from Horsarrieu (upper Ypresian, SW Aquitaine, France). *Revue de Micropaléontologie* 52, 267–288.
- Less, G. & Özcan, E. 2008: The late Eocene evolution of nummulitid foraminifer *Spiroclpeus* in the Western Tethys. *Acta Palaeontologica Polonica* 53, 303–316.
- Less, G., Özcan, E., Báldi-Beke, M. & Kollányi, K. 2007: Thanetian and early Ypresian orthophragmines (Foraminifera: Discocyclinidae and Orbitoclypeidae) from the central Western Tethys (Turkey, Italy and Bulgaria) and their revised taxonomy and biostratigraphy. *Rivista Italiana di Paleontologia e Stratigrafia* 113, 419–448.
- Less, G., Özcan, E., Papazzoni, C.A. & Stockar, R. 2008: The middle to late Eocene evolution of nummulitid foraminifer *Heterostegina* in the Western Tethys. *Acta Palaeontologica Polonica* 53, 317–350.
- Lunt, P. 2013: Foraminiferal micropalaeontology in SE Asia. In Bowden, A.J., Gregory, F.J. & Henderson, A.S. (eds): *Landmarks in Foraminiferal Micropalaeontology: History and Development*, 193–206. Micropalaeontological Society, Special Publications, London.
- Mathur, N.S., Juyal, K.P. & Kumar, K. 2009: Larger foraminiferal biostratigraphy of lower Paleogene successions of Zanskar Tethyan and Indus-Tsangpo Suture Zones, Ladakh, India in the light of additional data. *Himalayan Geology* 30, 45–68.
- McGowran, B. 2005: *Biostratigraphy*, 459 pp. Cambridge University Press, Cambridge.
- Meister, C. 2010: Worldwide ammonite correlation at the Pliensbachian Stage and Substage Boundaries (Lower Jurassic). *Stratigraphy* 7, 83–101.
- Molina, E., Alegret, L., Apellaniz, E., Bernaola, G., Caballero, F., Dinarès-Turell, J., Hardenbol, J., Heilmann-Clausen, C., Larrasoana, J.C., Luterbacher, H., Monechi, S., Ortiz, S., Orue-Etxebarria, X., Payros, A., Pujalte, V., Rodríguez-Tovar, F.J., Tori, F., Tosquella, J. & Uchman, A. 2011: The Global Stratotype Section and Point (GSSP) for the base of the Lutetian Stage at the Gorrondatxe section, Spain. *Episodes* 34, 86–108.
- Murphy, M.A. & Salvador, A. 1999: International stratigraphic guide – an abridged version. *Episodes* 22, 255–271.
- North American Commission on Stratigraphic Nomenclature 2005: North American stratigraphic code. *AAPG Bulletin* 89, 1547–1591.
- Nystuen, J.P. (ed.) 1989: Rules and recommendations for naming geological units in Norway, by the Norwegian Committee on Stratigraphy. *Norsk Geologisk Tidsskrift* 69(Suppl. 2), 1–107.
- Ogg, J.G. & Hinnov, L.A. 2012: Jurassic. In Gradstein, F.M., Ogg, J.G., Schmitz, M. & Ogg, G. (eds): *The Geologic Time Scale 2012*, 731–791. Elsevier, Amsterdam.
- Oppel, A. 1856–1858: Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands: nach ihren einzelnen Gliedern eingetheilt und verglichen. *Jahreshefte des Vereins für vaterländische Naturkunde Württembergs* 12–14, 1–857. (As a single volume, repaginated: Ebner und Seubert, Stuttgart. 1856: pp. 1–438; 1857: pp. 439–694; 1858: pp. 695–857.)

- d'Orbigny, A. 1850: *Paléontologie française: Terrains oolitiques ou jurassiques. 1 Céphalopodes*, 521–632. Masson, Paris.
- Page, K.N. 1995: Biohorizons and zonules: intra-subzonal units in Jurassic ammonite stratigraphy. *Palaeontology* 38, 801–814.
- Page, K.N. 2003: The Lower Jurassic of Europe: its subdivision and correlation. *Geological Survey of Denmark and Greenland Bulletin* 1, 23–59.
- Papazzoni, C.A., Moretti, A., Luciani, V., Fornaciari, E. & Giuberti, L. 2014: Correlation between shallow benthic zones and calcareous plankton zones at the Bartonian-Priabonian transition: Preliminary results from the Varignano section (Trento Province, Northern Italy). In Rocha, R., Pais, J., Kullberg, J.C. & Finney, S. (eds): *STRATI 2013*, 127–129. Springer Geology, Cham.
- Papazzoni, C.A., Čosović, V., Briguglio, A. & Drobne, K. 2017: Towards a calibrated larger foraminifer biostratigraphic zonation: celebrating 18 years of the application of Shallow Benthic Zones. *Palaïos* 32, 1–5.
- Paull, R.K. 1983: Evolution of a biostratigraphic zonation; lessons from Lower Triassic conodonts, U.S. Cordillera. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 71, 68–78.
- Payros, A., Bernaola, G., Orue-Etxebarria, X., Dinarès-Turell, J., Tosquella, J. & Apellaniz, E. 2007: Reassessment of the Early-Middle Eocene biomagnetostratigraphy based on evidence from the Gorronatxe section (Basque Country, western Pyrenees). *Lethaia* 40, 183–195.
- Payros, A., Tosquella, J., Bernaola, G., Dinarès-Turell, J., Orue-Etxebarria, X. & Pujalte, V. 2009: Filling the North European Early/Middle Eocene (Ypresian/Lutetian) boundary gap: insights from the Pyrenean continental to deep-marine record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280, 313–332.
- Pignatti, J.S. 1998: The philosophy of larger foraminiferal biozonation – a discussion. *Dela, Slovenska akademija znanosti in umetnosti, Opera, Academia Scientiarum et Artium Slovenica* 34, 15–20.
- Racey, A. 1994: Biostratigraphy and palaeobiogeographic significance of Tertiary nummulitids (foraminifera) from northern Oman. In Simmons, M.D. (ed.), *Micropalaeontology and Hydrocarbon Exploration in the Middle East*, 343–369. British Micropalaeontological Society Series, Chapman & Hall, London.
- Racey, A. 1995: Lithostratigraphy and larger foraminiferal (nummulitid) biostratigraphy of the Tertiary of northern Oman. *Micropalaeontology* 41 (suppl.), 1–123.
- Robinson, E. & Wright, R.M. 1993: Jamaican Paleogene larger foraminifera. In Wright, R.M. & Robinson, E. (eds): *Biostratigraphy of Jamaica. Memoirs of the Geological Society of America* 182, 283–345.
- Rodríguez-Pintó, A., Pueyo, E.L., Serra-Kiel, J., Samsó, J.M., Barnolas, A. & Pocolí, A. 2012: Lutetian magnetostratigraphic calibration of larger foraminifera zonation (SBZ) in the Southern Pyrenees: the Isuela section. *Palaeogeography, Palaeoclimatology, Palaeoecology* 333–334, 107–120.
- Rogov, M.A., Gulyaev, D.B. & Kiselev, D.N. 2012: Biohorizons as infrazonal biostratigraphic units: an attempt to refine the Jurassic stratigraphy based on ammonites. *Stratigraphy and Geological Correlation* 20, 211–229.
- Salvador, A. 1994: *International Stratigraphic Guide*, 2nd edn, 214 pp. Geological Society of America, Boulder.
- Schaub, H. 1951: Stratigraphie und Paläontologie des Schlierenflysches mit besonderer Berücksichtigung der palaeocaenen und untereocaenen Nummuliten und Assilinen. *Schweizerische Paläontologische Abhandlungen* 68, 1–222.
- Schaub, H. 1981: Nummulites et Assilines de la Téthys paléogène: taxinomie, phylogénese et biostratigraphie. *Schweizerische Paläontologische Abhandlungen* 104, 1–236.
- Scheibner, C. & Speijer, R.P. 2009: Recalibration of the Tethyan shallow benthic zonation across the Paleocene-Eocene boundary. *Geologica Acta* 7, 195–214.
- Schweigert, G. 2005: Albert Oppel (1831–1865) – ein Paläontologe von Weltruf an der Wende vom Katastrophismus zur Evolutionstheorie. *Jahreshefte der Gesellschaft für Naturkunde Württemberg* 161, 339–360.
- Scott, G.H. 2013: Biostratigraphy: interpretations of Oppel's zones. *Earth-Science Reviews* 126, 266–274.
- Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrández, C., Jauhri, A.K., Less, G., Pavlovec, R., Pignatti, J., Samsó, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J. & Zakrevskaya, E. 1998: Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France* 169, 281–299.
- Sigal, J. 1984: La zone en biostratigraphie: quelques réflexions et conventions. *Revue de Micropaléontologie* 27, 61–79.
- Stepanov, D.L. 1958: Printsipy i metody stratigraficheskikh issledovanii [Principles and Methods of Stratigraphic Studies]. *VNIIGRI Transactions* 113, 1–180.
- Streel, M., Higgs, K., Loboziak, S., Riegel, W. & Steemans, P. 1987: Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenno-Rhenish regions. *Review of Palaeobotany and Palynology* 50, 211–229.
- Vandenbergh, N., Hilgen, F.J. & Speijer, R.P. 2012: The paleogene period. In Gradstein, F.M., Ogg, J.G., Smith, A.G. & Ogg, G.M. (eds): *The Geologic Time Scale 2012*, 855–921. Elsevier, Amsterdam.
- van der Vlerk, I.M. 1955: Problems and principles of Tertiary and Quaternary stratigraphy. *Quarterly Journal of the Geological Society* 115, 49–63.
- van der Vlerk, I.M. & Umbgrove, J.H.F. 1927: Tertiaire gidsforaminiferen van Nederlandsch-Oost-Indië. *Wetenschappelijke Mededeelingen Dienst van den Mijnbouw in Nederlandsch-Indië* 6, 3–35.
- Walsh, S.L. 1998: Fossil datum and paleobiological event terms, paleontostratigraphy, chronostratigraphy, and the definition of Land Mammal 'Age' boundaries. *Journal of Vertebrate Paleontology* 18, 150–179.
- Walsh, S.L. 2000: Eubiostratigraphic units, quasibiostratigraphic units, and 'assemblage zones'. *Journal of Vertebrate Paleontology* 20, 761–775.
- Zeiss, A. 2003: The Upper Jurassic of Europe: its subdivision and correlation. *Geological Survey of Denmark and Greenland Bulletin* 1, 75–114.
- Zhamoida, A.I. (ed.) 2006: *Stratigraphic Code of Russia*, 3rd edn. English translation, 2012, 48 pp. VSEGEI Press, St. Petersburg (Interdepartmental Stratigraphic Committee of Russia).
- Zhang, Q., Willems, H. & Ding, L. 2013: Evolution of the Paleocene-Early Eocene larger benthic foraminifera in the Tethyan Himalaya of Tibet, China. *International Journal of Earth Sciences (Geologische Rundschau)* 102, 1427–1445.

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