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# 疑源类 *Ammonidium* Lister 1970 与相关种的厘定及其生物地层和古地理意义

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**摘要:**许多可归为疑源类 *Ammonidium* Lister 1970 的种被前人划为 *Multiplicisphaeridium* Staplin, 1961、*Baltisphaeridium* Eisenack 1958 ex Eisenack 1959 及其他相似属,在某种程度上缩小了其原有定义范围. 报道了采自新疆西准噶尔洪古勒楞组下段保存良好的 *Ammonidiumloriferum*、*A. sprucegrovense*, 通过相关文献引证对比,并结合剖面部分该属标本化石,对 *Ammonidium* 属征作了修订. 根据新属征特点,将 *Caiacorymbifer* Tappan and Loeblich, 1971, *Gracilisphaeridium* Eisenack and Cramer, 1973, *Naevisphaeridium* Wicander, 1974, *Puteoscorrum* Wicander and Loeblich, 1977, *Craterisphaeridium* Deunff, 1981, *Pertusisphaeridium* Turner, 1986 和 *Martinsphaeridium* Sarjeant and Vavrdová, 1997 等相似属纳入 *Ammonidium* 属的晚出异名. *Ammonidium sprucegrovense* var. *polyankistrum* Wicander and Loeblich, 1977 由种级降为了变种级. 建立 1 个新种: *Ammonidium levigatum* n. sp., 前人报道的部分标本被误归为 *A. loriferum* 或 *A. sprucegrovense*. 新种 *Ammonidium levigatum* n. sp. 在全球晚泥盆世古大陆边缘具有全球分布特征,是识别晚泥盆世疑源类的标准化石之一.

**关键词:** 疑源类; *Ammonidium*; 系统分类学; 生物地层; 古地理; 新疆北部.

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## Taxonomic Reconsideration of *Ammonidium* Lister 1970 and Related Species and Its Biostratigraphical and Palaeogeographical Implication

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**Abstract:** Many species that can be attributed to *Ammonidium* Lister, 1970 have been differently assigned to *Multiplicisphaeridium* Staplin, 1961, *Baltisphaeridium* Eisenack, 1958 ex Eisenack, 1959 and other similar genera, which, to some extent, narrowed the original definition. The diagnosis of *Ammonidium* is emended here in based on reference comparison

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and some *Ammonidium* taxa collected recently from the lower part of the Hongguleleng Formation, NW Xinjiang. This paper considers *Caiacorymbifer* Tappan and Loeblich 1971, *Gracilisphaeridium* Eisenack and Cramer 1973, *Naevisphaeridium* Wicander 1974, *Puteoscortum* Wicander and Loeblich 1977, *Craterisphaeridium* Deunff 1981, *Pertusisphaeridium* Turner 1986, and *Martinsphaeridium* Sarjeant and Vavrdová 1997 are junior synonyms of *Ammonidium*. The taxonomical ranks of *Ammonidium sprucegrovense* var. *polyankistrum* Wicander and Loeblich, 1977 are changed from the *species* to the *varietas* level. A new species is proposed, i.e., *Ammonidium levigatum* n. sp., which may have been erroneously identified as *A. loriferum* (Deunff) Hashemi and Playford 1998 or *A. sprucegrovense* (Staplin) Lister 1970 in many publications. *Ammonidium levigatum* n. sp. is widely distributed in the margins of palaeocontinents and is an important stratigraphical index fossil for the Late Devonian.

**Key words:** *Ammonidium*; acritarchs; taxonomy; biostratigraphy; palaeogeography; palaeobiology; NW China.

## 0 引言

疑源类被广泛应用于生物地层对比、生物古地理和古环境的识别,是重要的微体化石类群。目前疑源类的分类主要基于其表型特征,而非生物亲缘关系(Stricanne and Servais, 2002)。和大多数化石一样,如何将疑源类根据形态特征进行有效分类,仍是近半个世纪以来疑源类学者面临的重要议题(如:Eisenack *et al.*, 1973, 1976; Fensome *et al.*, 1990; Díez and Cramer, 1977; Sarjeant and Stancliffe, 1994; Sarjeant and Vavrdová, 1997; Servais *et al.*, 2007; Lei *et al.*, 2013; Kroeck *et al.*, 2020; 李猛等,2021; Wu *et al.*, 2021)。

棘刺类 *Ammonidium* Lister, 1970, 因具球形/椭球形的膜壳外形及仅一级分枝结构而易被识别,在寒武纪—泥盆纪具有较广的地理分布范围。据现有资料记载, *Ammonidium* 最早出现于加拿大 Alberta, 即 *Multiplicisphaeridium canadense* Staplin, Jansonius, and Pocock, 1965 (Eisenack *et al.*, 1973), 最晚记载于该地密西西比亚系杜内阶(Tournaisian) (*Multiplicisphaeridium winslowii* Staplin, Jansonius, and Pocock, 1965). *Ammonidium* 能沿用至今,已被多数学者所接受,但由于原始定义简单,部分内容宽泛,很多后期新发现的属种被不同地归为 *Ammonidium*、*Multiplicisphaeridium* Staplin, 1961 或 *Baltisphaeridium* Eisenack 1958 ex Eisenack 1959 及其他相似属,有时被定义为新属,如 *Martinsphaeridium* Sarjeant and Vavrdová 1997. 许多早期外文发表的成果已很难找到原始资料,本文的目的在于对 *Ammonidium* 属征进行重新修订,并就采自新疆北部洪古勒楞组下段的与 *Ammonidium* 有关的疑源类进行描述和讨论,揭示 *Ammonidium* 属的生物地层及古地理特征和意义。

## 1 材料与方法

本文所用数据部分来自文献资料,资料源于 *Ammonidium* 和 *Multiplicisphaeridium* 命名原刊 (Staplin, 1961; Lister, 1970)、前人所报道全球各地分布有 *Ammonidium* 及 *Multiplicisphaeridium* 属等属种及疑源类突起末端具有分枝结构的相似属种相关论著(如 Eisenack *et al.*, 1973; Sarjeant and Vavrdová, 1997),部分采自新疆北部和布克赛尔蒙古自治县境内根那仁剖面( $46^{\circ}37'24.24''N$ ;  $86^{\circ}4'36.48''E$ ; 图1),剖面自下而上,分别出露中—上泥盆统的朱鲁木特组、洪古勒楞组和黑山头组。前人将洪古勒楞组分为5个岩性段(马学平等,2013;宗普等,2014; Ma *et al.*, 2017),自下而上分别为:下段(杜古尔段、萨尔巴段、龙口段)、中段(乌兰段)和上段(查斯段),样品采自洪古勒楞组下段(法门阶)(图2)。孢粉样品的准备过程采用标准的孢粉处理方法(Wood *et al.*, 1996),处理过程包括 HCl-HF-HCl(每一个步骤后做中和处理),重液浮选,最后用蒸馏水中和,该过程在中国地质大学(武汉)微体古生物实验室完成。有机质残渣经  $15\text{ }\mu\text{m}$  和  $50\text{ }\mu\text{m}$  孔径过筛处理,薄片制作及拍照(采用 Zeiss Axio Imager 显微镜),在法国里尔大学 Evo-Eco-Paleo Unit (EEP)-UMR CNRS 8198 实验室完成。洪古勒楞组下段下部以黑灰色、深黑色孢子居多,下段上部以黄色、黄褐色疑源类为主。疑源类总体保存状况较好,样品保存在山西财经大学资源环境学院。

## 2 *Ammonidium* 属

### 2.1 历史回顾

*Ammonidium* Lister, 1970 的模式种为 *Ammonidium microcladum* (Downie) Lister, 1970, “Ammon”来源于埃及“阿蒙”神,“idium”是甲藻和浮游

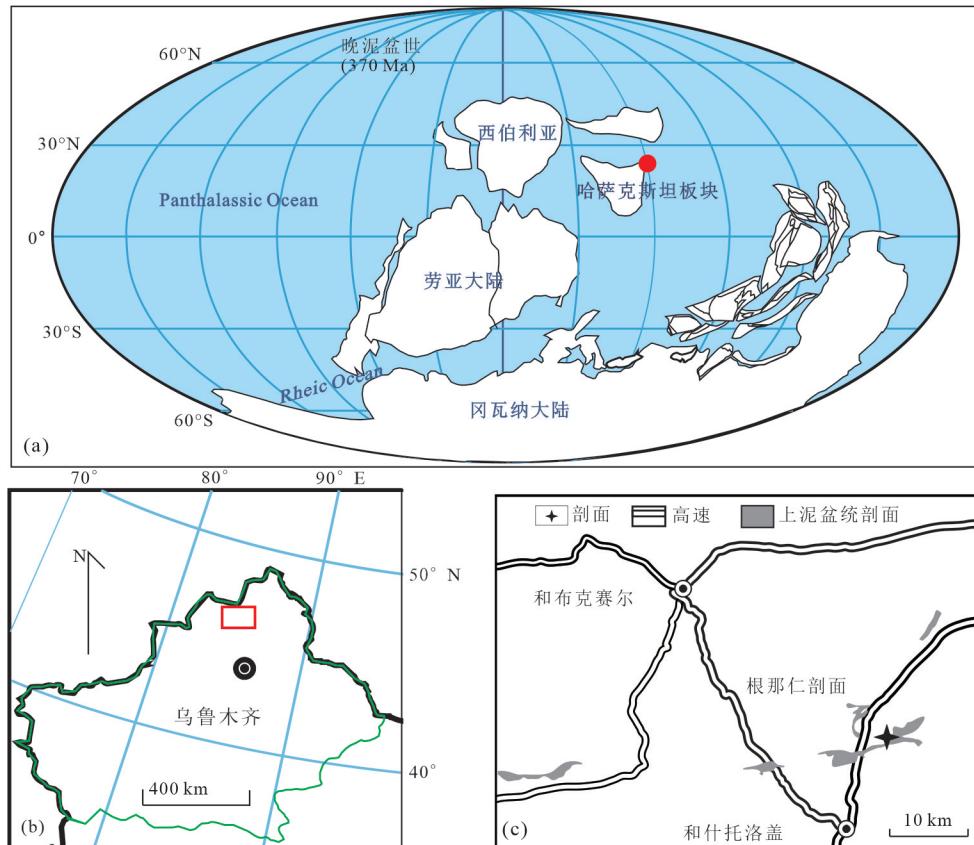


图1 (a)晚泥盆世古地理图(修改自 Boucot *et al.*, 2013),显示孢粉样品采集地哈萨克斯坦板块的位置;(b)研究剖面在新疆的位置;(c)根那仁剖面所在详细位置及西准噶尔上泥盆统出露情况

Fig. 1 (a) Late Devonian palaeogeographic map(modified from Boucot *et al.*, 2013), showing the location of the Kazakhstan plate where palynological samples have been collected;(b) the geographical location in Xinjiang; (c) Detailed location of the studied section and Upper Devonian outcrops of Western Junggar

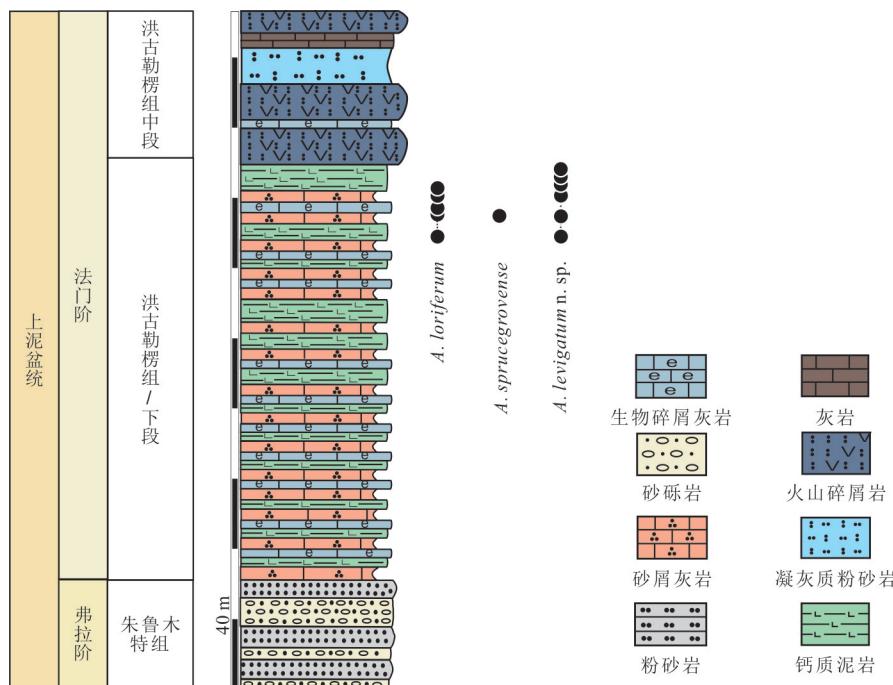
植物等中较常用的词尾.该种首次报道于英格兰 Shropshire 地区的温洛克页岩区(Wenlock Shales) (Lister, 1970),建属时与 *Ammonidium rigidum* var. *ludloviensis* Lister, 1970 及 *Ammonidium* sp. 同时建立.

Lister (1970) 认为 *Ammonidium* 与 *Multiplicisphaeridium* 最大的不同在于前者突起的末端仅有一级分枝结构(图3),且所有突起的形态基本一致,即突起的同型性是 *Ammonidium* 与 *Multiplicisphaeridium* 相区别的典型特征.

除了以上观点外,Loeblich and Wicander(1976)还认为该突起末端的分叉类型是一种简单的远端分化,其分枝较小、末端尖锐,单个种的分叉仅有一种类型,而 *Multiplicisphaeridium* 突起末端的分枝类型为多变形态.除此以外,Loeblich and Wicander (1976)还指出,*Baltisphaeridium* 属与 *Ammonidium* 属的不同在于后者的突起可与膜壳自由连通,而前

者不具备该特征.

*Ammonidium* 属的部分种曾长期被归为 *Multiplicisphaeridium* 或 *Baltisphaeridium* (表 1 和表 2; Lister, 1970; Eisenack *et al.*, 1973). Eisenack *et al.* (1976) 曾认为该属突起的分叉结构很难作为属级划分的特征,且地理“种”的突起并不具备同型性特征,因此认为 *Ammonidium* 应为 *Multiplicisphaeridium* 的晚出异名.除以上观点外,大部分学者还是认同 *Ammonidium* 作为独立属存在的合理性.除了具有一级分枝结构以外,Dorning(1981)还将 *Ammonidium* 膜壳表面的光滑、瘤点及小凹穴特征作为定义该属的基本特征.Le Hérisse(1989)对该属膜壳表面特征作了修订,认为膜壳表面光滑、外壁薄、具小型瘤点(microgranulate)、粗糙(scabrate)或具皱状纹饰(microrugulate).Sarjeant and Vavrdová(1997)除了认为 *Ammonidium* 突起末端的分枝形态通常具有一致性以外,还将突起长度约束为应超过膜壳

图 2 根那仁剖面洪古勒楞组岩性与 *Ammonidium* 属的分布Fig. 2 Lithostratigraphy and *Ammonidium* distribution of the Hongguleleng Formation in the Gennaren section

直径的 20%，分枝的数量约束为 2~6，分枝末端或具备二次分叉的可能性。本文依据 *Ammonidium* 的形态特征，对符合该属特征的 *Ammonidium*、*Multiplicisphaeridium* 及 *Baltisphaeridium* 等属种的部分种作了重新归纳，*Ammonidium* 已有种见表 1，新纳入 *Ammonidium* 的种见表 2。

### 3 系统描述

- Acritarcha Evitt 1963  
***Ammonidium*** Lister, 1970  
 模式种 *Ammonidium microcladum* Downie, 1963 emend. Lister, 1970 nov. emend.  
 1970 *Ammonidium* Lister, pp. 48—49.  
 1971 *Caiacorymbifer* T appan and Loeblich, pp. 390—391.  
 1973 *Gracilisphaeridium* Eisenack and Cramer (in Eisenack *et al.*, 1973, pp. 510).  
 1974 *Naevisphaeridium* Wicander, pp. 30.  
 1977 *Puteoscortum* Wicander and Loeblich, pp. 148.  
 1981 *Craterisphaeridium* Deunff, pp. 67.  
 1986 *Pertusisphaeridium* Turner, pp. 606.  
 1997 *Martinsphaeridium* Sarjeant and Vavrdová, pp. 27.

原始描述 (Lister, 1970)：“Vesicle hollow, spherical to ellipsoidal, single-walled; vesicle wall smooth or sculptured. Processes numerous, evenly spaced, more or less rigid, hollow, tapering communicating freely with the vesicle cavity; distally the processes have equifurcate terminations. Excystment by cryptosuture, apical or near-equatorial”。

修订属征 (Le Hérissé, 1989)：“Vesicle spherical with circular or ellipsoidal outline with wall single, thin, smooth or lightly ornamented (microgranulate, scabrate, microrugulate), bearing numerous processes of variable length, equidistant, homomorphic, whose distal extremity is divided into a cluster of 3 to 5 short branches, extended in a single plane; the branches may be divided at tip; on each process the branches are of equal length and for a given specimen the branches are of equal length and for a given specimen the branches appear identical; the stems of the processes may display a light granulation; the system of opening is of a simple slit type with slight ridges on the margins”。

修订属征 (Sarjeant and Vavrdová, 1997)：“Vesicle hollow, spherical to ellipsoidal, single-walled or apparently so. Processes moderately numerous to nu-

表1 *Ammonidium* 属已有种列表  
Table 1 List of *Ammonidium* acritarch species described in the literature

种名	原属名	作者和年份
<i>A. alloiteui</i>	<i>Micrhystridium; Baltisphaeridium; Ammonidium</i>	Deunff(1955); Martin(1981)
<i>A. belmonte</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Cramer(1970); Sarjeant and Vavrdová(1997)
<i>A. belmontiforme</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Tynni(1975); Sarjeant and Vavrdová(1997)
<i>A. carrascum</i>	<i>Baltisphaeridium; Multiplicisphaeridium; Ammonidium</i>	Cramer(1966); Sarjeant and Vavrdová(1997)
<i>A. crinitum</i>	<i>Micrhystridium; Multiplicisphaeridium?; Ammonidium</i>	Grishina and Klenina(1981); Sarjeant and Vavrdová(1997)
<i>A. cornutum</i>	<i>Ammonidium</i>	Loeblich and Wicander(1976)
<i>A. conicum</i>	<i>Ammonidium</i>	Pôthe de Baldis(1998)
<i>A. exoticum</i>	<i>Baltisphaeridium; Ammonidium</i>	Deunff(1965a); Lister(1970)
<i>A. furtivum</i>	<i>Ammonidium</i>	Playford and Martin(1984)
<i>A. grosjeani</i>	<i>Baltisphaeridium; Ammonidium</i>	Stockmans and Willière(1962a); Martin(1981)
<i>A. hamatum</i>	<i>Ammonidium</i>	Wicander(1974)
<i>A. inornatum</i>	<i>Ammonidium</i>	Colbath(1990)
<i>A. iowaensis</i>	<i>Ammonidium</i>	Wicander and Wood(1997)
<i>A. lewisii</i>	<i>Hystrichosphaeridium; Baltisphaeridium; Ammonidium</i>	Deunff(1954); Lister(1970)
<i>A. loriferum</i>	<i>Baltisphaeridium; Ammonidium</i>	Deunff(1965b); Hashemi and Playford(1998)
<i>A. ludoviense</i>	<i>Ammonidium</i>	Lister(1970); Dorning(1981)
<i>A. microcladum</i>	<i>Baltisphaeridium; Ammonidium</i>	Downie(1963); Lister(1970)
<i>A. maravillosum</i>	<i>Multiplicisphaeridium; Baltisphaeridium; Ammonidium</i>	Cramer(1969); Thusu(1973); Diez and Cramer(1977)
<i>A. maritimum</i>	<i>Ammonidium</i>	Martin(1984)
<i>A. macilentum</i>	<i>Ammonidium</i>	Playford and Martin(1984)
<i>A. multipugiunculatum</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Cramer and Diez(1977); Rubinstein <i>et al.</i> (1999)
<i>A. olsztynense</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Górká(1979); Sarjeant and Vavrdová(1997)
<i>A. palmitella</i>	<i>Baltisphaeridium; Ammonidium</i>	Cramer and Diez(1972); Dorning(1981)
<i>A.? pequenhum</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Cramer and Diez(1972); Sarjeant and Vavrdová(1997)
<i>A. sprucegrovense</i>	<i>Multiplicisphaeridium; Puteoscutum; Ammonidium</i>	Staplin(1961); Lister(1970)
<i>A. truncatum</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Staplin(1961); Sarjeant and Vavrdová(1997)
<i>A. uncinum</i>	<i>Ammonidium</i>	Loeblich and Wicander(1976)
<i>A.? variabile</i>	<i>Multiplicisphaeridium; Ammonidium</i>	Lister(1970); Sarjeant and Vavrdová(1997)
<i>A. waldronense</i>	<i>Caiacorymbifer; Ammonidium</i>	Tappan and Loeblich(1971); Dorning(1981)

merous, their length typically exceeding 20% of the vesicle diameter. They are slender, showing only a slight proximal inflation, and hollow, their cavity communicating directly with the vesicle interior. The processes are usually homomorphic, but may show a restricted degree of variation; they are closed distally and exhibit a single order of branching confined to the distal extremity. Distal branching is usually uniform, into a low number of branches (2 to 6); occasionally a few processes may be acuminate. The branches are typically of equal or near-equal length and may show secondary division into branchlets; they show no linkage by trabeculae with other processes and are not enclosed within an ectilemma. Eilemma and surfaces of

processes laevigate or with inconspicuous ornamentation, but not striate or areolate and not exhibiting any pattern of indentations. Excystment by cryptosuture".

新修订属征膜壳呈圆形至亚圆形,原始呈球形。膜壳外壁光滑或具纹饰(小型瘤点、条纹状、凹穴状或网纹状);突起同型、中空(可与膜壳自由连通),互相分离,均匀分布,间距约3~10 μm,末端具有一级分枝结构;突起的基部微扩大,末端具2~8个等长或近等长、易弯曲的分枝,分枝末端可偶见小型二级分枝。突起长度通常小于膜壳直径[in English : Vesicle circular to subcircular in outline, originally spheroidal. Vesicle wall smooth or sculptured (microgranulate, striate, foveolate or areolate sculpture); Processes discrete, homomorphic, evenly dis-

表 2 *Ammonidium* 属新纳入的种Table 2 Species newly included of *Ammonidium* in this study

种名	原属名	作者和年份
<i>A. acaciaense</i>	<i>Multiplicisphaeridium</i>	Playford and Martin(1984)
<i>A. bifurcatum</i>	<i>Multiplicisphaeridium</i>	Staplin <i>et al.</i> (1965)
<i>A. bonitum</i>	<i>Baltisphaeridium; Multiplicisphaeridium; Thy- sanoprobolus</i>	Jardiné and Yapaudjian(1968); Cramer(1970); Loeblich and Tappan (1970); Eisenack <i>et al.</i> (1973)
<i>A. brevifurcatum</i>	<i>Hystrichosphaeridium; Baltisphaeridium; Mul- tiplicisphaeridium</i>	Eisenack(1954); Downie and Sarjeant(1963); Eisenack <i>et al.</i> (1973)
<i>A. canadense</i>	<i>Multiplicisphaeridium</i>	Staplin <i>et al.</i> (1965); Eisenack <i>et al.</i> (1973)
<i>A. dispar</i>	<i>Pertusisphaeridium</i>	Turner(1986)
<i>A. estrellaferum</i>	<i>Baltisphaeridium; Multiplicisphaeridium</i>	Cramer(1966); Eisenack <i>et al.</i> (1973)
<i>A. furcatum</i>	<i>Priscogalea; Baltisphaeridium; Multiplici- sphaeridium</i>	Deunff, 1961, 1964; Eisenack <i>et al.</i> (1973)
<i>A. encantador</i>	<i>Baltisphaeridium; Gracilisphaeridium</i>	Cramer(1970); Eisenack <i>et al.</i> (1973)
<i>A. jardineae</i>	<i>Baltisphaeridium; Multiplicisphaeridium</i>	Jardiné and Yapaudjian(1968); Cramer(1970); Eisenack <i>et al.</i> (1973)
<i>A. kahleri</i>	<i>Baltisphaeridium; Multiplicisphaeridium</i>	Bachmann and Schmid(1964); Eisenack <i>et al.</i> (1973)
<i>A. lichenoides</i>	<i>Multiplicisphaeridium; Martinsphaeridium</i>	Uutela and Tynni(1991); Sarjeant and Vavrdová(1997)
<i>A. micropilaris</i>	<i>Baltisphaeridium; Multiplicisphaeridium</i>	Cramer(1970); Eisenack <i>et al.</i> (1973)
<i>A. oligofurcatum</i>	<i>Hystrichosphaeridium; Baltisphaeridium; Vis- bysphaera; Multiplicisphaeridium</i>	Eisenack(1954); Downie(1963); Eisenack <i>et al.</i> (1973)
<i>A. parvipinnatum</i>	<i>Multiplicisphaeridium; Martinsphaeridium</i>	Uutela and Tynni(1991); Sarjeant and Vavrdová(1997)
<i>A. parvispinosum</i>	<i>Multiplicisphaeridium; Martinsphaeridium</i>	Uutela and Tynni, 1991; Sarjeant and Vavrdová(1997)
<i>A. piriferumgotlandicum</i>	<i>Multiplicisphaeridium; Baltisphaeridium</i>	Cramer(1970); Eisenack <i>et al.</i> (1973)
<i>A. piriferumpiriferum</i>	<i>Hystrichosphaeridium; Baltisphaeridium; Mul- tiplicisphaeridium</i>	Eisenack(1954); Downie and Sarjeant(1963); Eisenack <i>et al.</i> (1973)
<i>A. sprucegrovense</i> var. <i>polyankistrum</i> var. nov.	<i>Puteoscortum</i>	Staplin(1961); Wicander and Loeblich(1977); Wicander and Playford (2013)
<i>A. plenilunium</i>	<i>Naevisphaeridium</i>	Wicander(1974)
<i>A. pustulatum</i>	<i>Baltisphaeridium; Multiplicisphaeridium</i>	Schultz(1967); Eisenack <i>et al.</i> (1973)
<i>A. raplaense</i>	<i>Multiplicisphaeridium; Martinsphaeridium</i>	Uutela and Tynni(1991); Sarjeant and Vavrdová(1997)
<i>A. winslowii</i>	<i>Gorgonisphaeridium; Multiplicisphaeridium</i>	Staplin <i>et al.</i> (1965); Eisenack <i>et al.</i> (1973)
<i>A. williereae</i>	<i>Puteoscortum</i>	Martin(1981)

tributed, 3 to 10  $\mu\text{m}$  apart, and hollow (communicating unimpeded with the vesicle cavity), whose distal extremity divided into only one order of branching; the base of the processes are enlarged, and the distal branching is divided into a cluster of 2-8 equal or near-equal length, flexible, and recurved branches, which may occur minor secondary division, occasionally, but no great variability of branching exhibited into branchlets at tip in a given specimen. The processes are usually no longer than the diameter of the vesicle.]

讨论在 *Ammonidium* 新的属征中, 具四面体胞形(非球形—类球形)特征的种, 如: ?*Multiplicisphaeridium cazurrum* (Cramer, 1966) Eisenack et

al., 1973, *Multiplicisphaeridium continuatum* Kjellström, 1971 和 *Multiplicisphaeridium sartbernardense* Eisenack *et al.*, 1973 (见 Eisenack *et al.*, 1973, pp. 563、571、790)并不属于该属的范畴. 本文保留其突起同型性特征, 并允许突起末端的分枝具细微变化. *Naevisphaeridium* Wicander, 1974 (Wicander, 1974, pp. 30, pl. 15, 4-6) 表面具有椭圆形的压痕, 其余特点与 *Ammonidium* 属征无异. *Puteoscortum* Wicander and Loeblich, 1977 具有圆形至亚圆形的轮廓, 外壁呈孔穴一网状, 具一定数量的柱状、中空、光滑的突起. 突起的末端具有 6 个分枝. 这里值得一提的是, Lister (1970) 在建立 *Ammonidium* 时, 仅强调其表面光滑或具纹饰, 并未将具有凹穴一网格状纹饰特征的属种排除在外, 因此

本文将 *Puteoscortum* 视为 *Ammonidium* 的晚出异名。*Craterisphaeridium* Deunff, 1981 呈球形, 具有中空的外表, 膜壳表面具凹穴状纹饰。突起中空, 基部扩大呈根状; 突起末端分叉为易弯曲的细丝状。*Craterisphaeridium* 曾被 Wicander and Playford (2013) 划归为 *Puteoscortum* 的晚出异名, 因此, *Craterisphaeridium* 属也应为 *Ammonidium* 的晚出异名。此外, *Martinsphaeridium* Sarjeant and Vavrdová, 1997 的建立基于报道于澳大利亚西部的 *Ammonidium macilentum* Playford and Martin, 1984 (Playford and Martin, 1984, pp. 192, fig. 5A~5F)。该属的特点是突起较短, 突起的数量较多。*Pertusisphaeridium* Turner, 1986 外形呈球形, 中空、单壁。膜壳表面具瘤点状突起、末端尖锐, 此外具有长条状突起, 突起中空, 可与膜壳相互连通, 该突起末端分叉、分枝结构细长、易弯曲。*Gracilisphaeridium* Eisenack and Cramer, 1973 的特点是突起相对较短、细长、中空, 突起的末端具有环形羽状轮廓, 该属特点与 *Ammonidium* 属相符合 (Hill, 1974, p. 11; Fensome et al.,

1990, 58), 以上 3 个属在本文均归入 *Ammonidium* 的晚出异名。依据相似的形态、相似的膜壳直径、突起数量、突起长度、突起基部直径和突起末端直径等指标, 本文将表 3 已知种列为晚出异名。

*Ammonidium loriferum* (Deunff) Hashemi and Playford (1998)

模式种 *Ammonidium microcladum* (Downie) Lister (1970)

图版 1, 13—18

1965b *Baltisphaeridium loriferum* Deunff, pp. 163; figs. 6—8.

1970 *Ammonidium loriferum* (Deunff) Lister, pp. 49.

1973 *Multiplicisphaeridium loriferum* (Deunff) Eisenack et al., pp. 675.

1996 *Ammonidium garrasinoi* Ottone, pp. 121, pl. 4, figs. 1~3, 6, 7.

1998 *Ammonidium loriferum* Hashemi and Playford, pp. 140, pl. 5, figs. 1, 2.

表 3 部分 *Ammonidium* 种的新分类

Table 3 New classification of selected species of *Ammonidium*

新种名	原种名	V*	PN*	PL*	PB*	PD*	作者和年份
<i>Ammonidium aduncum</i>	<i>A. listeri</i>	19~34	>50	3~5	0.6	<1	Smelror(1987)
	<i>A. aduncum</i>	33~75	>50	2~4	0.5~2.0	ca. 1	Playford and Martin(1984)
	<i>A. ballistum</i>	38~59	>50	3~10	1.0~1.5	<1	Ottone et al.(1992)
<i>Ammonidium grosjeani</i>	<i>A. grosjeani</i>	24~34	35~45	10~15	1~2	0.5~3	Stockmans and Williere(1962a); Eisenack et al.(1973); Martin(1981)
	<i>A. hydraferum</i>	ca. 25	30~40	8~13	2~3	3~5	Stockmans and Williere(1962a); Lister(1970)
<i>Ammonidium ludloviense</i>	<i>A. ludloviense</i>	21~35	35~45	ca. 4	2~3	ca. 1	Lister(1970); Dorning(1981)
	<i>M. saharicum</i>	21~34	ca. 30	4~6	2~3	<1	Lister(1970)
<i>Ammonidium loriferum</i>	<i>A. loriferum</i>	30~40	ca. 9	15~20	3~4	4~5	Hashemi and Playford(1998)
	<i>A. garrasinoi</i>	29~40	8~10	10~20	2~3	5~6	Ottone(1996)
<i>Ammonidium piriferum gotlandicum</i>	<i>M. erraticum</i>	ca. 45	ca. 25	20~30	2~3	<1	Eisenack et al.(1973)
	<i>M. piriferum gotlandicum</i>	ca. 60	ca. 22	10~18	3~5	2~10	Eisenack et al.(1973)
	<i>M. gotlandicum</i>	ca. 50	>25	ca. 6	2~3	<1	Eisenack et al.(1973)
	<i>M. piriferum hispanicum</i>	ca. 60	ca. 24	10~20	2~5	1~5	Eisenack et al.(1973)
<i>Ammonidium piriferumpiriferum</i>	<i>M. piriferumpiriferum</i>	60~90	ca. 18	15~20	5~8	1~5	Eisenack et al.(1973)
<i>Ammonidium sprucegrovense</i>	? <i>A. paleozoicum</i>	ca. 30	ca. 11	ca. 10	3~5	3~5	Sarjeant and Vavrdová(1997)
	? <i>A. sprucegrovense</i>	30~43	12~18	17~25	2~3	3~5	Martin(1981)
	<i>B. microfurcatum</i>	ca. 22	15~20	12~15	3~6	ca. 6	Deunff(1957); Fensome et al.(1990)
<i>Ammonidium sprucegrovense</i> var. <i>polyankistrum</i>	<i>Puteoscortum polyankistrum</i>	38~58	15~18	13~24	2.5~5.0	3~8	Wicander and Loeblich(1977)

注: V. 膜壳直径(diameter of the vesicle); PN. 突起的数量(number of processes); PL. 突起的长度(length of the processes); PB. 突起基部的直径(diameter of the bases of the processes); PD. 突起末端的直径(diameter of the distal end of the processes)

- 1996 *Ammonidium loriferum*, Ghavidel-Syooki, pp. 410, pl. 7, fig. 8.
- 2001 *Ammonidium loriferum*, Ghavidel-Syooki, pp. 44, pl. 3, fig. 1
- 2005 *Ammonidium loriferum*, Filipiak, pp. 14, pl. II, figs. 3, 8.
- 2017 *Ammonidium loriferum - Ammonidium garrasinoi*, di Pasquo et al., pp. 198, pl. 1, fig. 1
- 2018 *Ammonidium loriferum - Ammonidium garrasinoi*, Noetinger et al., pp. 99, pl. I, fig. 1.
- 2020 *Ammonidium garrasinoi*, de Andrade et al., 2020, pp. 13, pl. 2, N.
- 2020 *Ammonidium loriferum*, de Andrade et al., 2020, pp. 14, pl. 3, G.

原始种征(Deunff, 1965b):“Coque sphéridale à section schématiquement polygonale vue en coupe optique, comportant une dizaine d'appendices apparemment obturés à la base, terminés par de petites lanières groupées en forme de fouet. Diamètre de la coque=30 à 40 μ. Longueur des appendices=15 à 20 μ. Diamètre de base=3 à 4 μ. Nombre de lanières terminales=3 à 5 μ. Longueur des lanières=4 à 5 μ”。

修订种征(Hashemi and Playford, 1998):“Vesicle circular to hexagonal in outline, originally spheroidal to polyhedral. Eilyma 0.8 to 1 μm thick, psilate or very finely pitted (?corrosion effect). Processes discrete, homomorphic, spine-like in gross form, 9 to 10 per vesicle and well-differentiated from the latter, hollow (freely communicating with vesicle interior), ± rigid, same thickness as eilyma but superficially granulate-finely echinate. Proximal process contacts angular to slightly curved; distal termini palmately branched (4 to 6 conical branches, 3 to 7 μm long, apices acuminate). Process dimensions: length 16 to 21 μm, basal diameter 3 to 3.5 μm, gradual distal taper (diameter decreasing to 0.8 to 1.2 μm near point of branching). Processes fairly evenly distributed, 5 to 10 μm apart. No excystment structure observed”。

特征(新修订)原始膜壳呈球形,单壁,具有非常细小的点状纹饰;突起8~10条,中空、分离、同型、末端变尖,均匀分布,突起的基部扩大,呈根状;突起末端分叉,分枝结构纤细、易弯曲,呈掌状,分

枝数量约3~5,等长或近等长(in English : Vesicle originally spherical in outline, single-walled, and very finely pitted; the processes are hollow, discrete, homomorphic, tapering, and evenly distributed, 8 to 10 in number per vesicle, the base of the processes are enlarged to form root-like structures; the distal branching is divided into a cluster of 3 to 5 palmately, equal or near-equal length, and recurved filaments.)。

尺寸(基于5个标本)膜壳直径:40 μm(45.98 μm)50 μm;突起长度:17 μm(17.6 μm)21 μm;突起基部宽度:3 μm(4.6 μm)5 μm;分枝长度:4 μm(4.5 μm)5 μm。

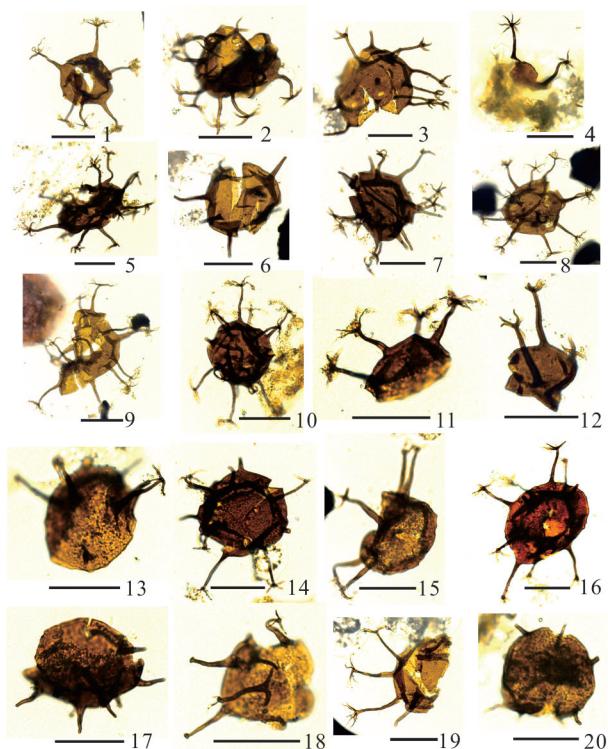
讨论 Deunff (1965b) 并没有 *Baltispheridium loriferum* 的详细描述,也无照片(仅有3张手绘素描图). Ottone (1996)凭借 *Ammonidium garrasinoi* 的形态轮廓呈多边形而非球形,而与 *Ammonidium loriferum* 相区别.di Pasquo et al.(2017)报道的美国 Montana 州的标本及 Noetinger et al.(2018)报道的阿根廷标本就将二者视为同一种,其多边形而非圆形/椭圆形的外形特点可能被夸大,因此本文将二者视为同一种.*Ammonidium loriferum* 与 *Puteoscor-tum polyankistrum* Wicander and Loeblich, 1977 的不同在于膜壳纹饰,后者呈凹穴—网格状(Wicander and Loeblich, 1977, pp. 148). 报道于新疆北部布龙果尔剖面的标本(Stachacz et al., 2021, pp. 734, fig. 9r)膜壳表面具有明显地光滑特征,本文不认为其属于 *Ammonidium loriferum*,而属于新定种 *A. levigatum* n. sp,详述见后文.

产地与时代法国 Boulonnais 弗拉阶(Deunff, 1965b);伊朗法门阶(Ghavidel-Syooki and Owens, 2007; Hashemi and Playford, 1998; Taherian et al., 2021);美国 Montana 州中部法门阶(di Pasquo et al., 2017);波兰中部法门阶(Filipiak, 2005);阿根廷中—上泥盆统(Ottone, 1996; Noetinger et al., 2018);巴西 Paranaíba 盆地吉维特阶—弗拉阶(de Andrade et al., 2020);玻利维亚、阿根廷吉维特阶—法门阶(di Pasquo et al., 2015);新疆西准噶尔法门阶。

*Ammonidium sprucegrovense* (Staplin) Lister, 1970

图版 1, 19

1961 *Multiplicisphaeridium? sprucegrovensis*



图版1 所有标本均采自新疆西准噶尔根那仁剖面洪古勒楞组下段上部

Plate 1 All the samples were collected at the upper part of the lower member of the Hongguleleng Fm. from the Genaren section

1~12. *Ammonidium levigatum* sp. nov. 1. GNR62-92, 237.7 m; 2. GNR58-2, 224.7 m; 3. GNR58-33, 224.7 m; 4. GNR50-98, 224.7 m; 5. GNR55-3, 216.1 m; 6. GNR58-1, 224.7 m; 7. GNR58-25, 224.7 m; 8. GNR62-4, 237.7 m; 9. GNR62-5, 237.7 m; 10. GNR62-2, 237.7 m; 11. GNR62-91, 237.7 m; 12. GNR58-5, 224.7 m; 13~18. *Ammonidium loriferum* (Deunff) Hashemi and Playford(1998). 13. GNR50-5, 200 m; 14. GNR50-4, 200 m; 15. GNR55-1, 216.1 m; 16. GNR50-1, 200 m; 17. GNR61-1, 234.2 m; 18. GNR61-1, 234.2 m; 19. *Ammonidium sprucegrovense*, GNR55-4, 216.1 m; 20. *Ammonidium* sp., GNR50-96, 200 m (图中比例尺=20 μm)

Staplin, pp. 411, pl. 48, fig. 22; pl. 49, fig. 6, text-fig. 9j.

1970 *Ammonidium sprucegrovensis*(Staplin, 1961) Lister, pp. 49.

1981 *Ammonidium sprucegrovense*Martin, pp. 12, pl. 1, figs. 13, 15.

1982 *Ammonidiumsprucegrovense*Martin, fig. 1; pl. 2, fig. 1.

1986 *Craterisphaeridiumsprucegrovense*(Staplin) Turner, pp. 602—606, pl. 1, figs. 1~6; pl. 2, figs.

1~4.

1988 *Craterisphaeridiumsprucegrovense*(Staplin) Lu and Wicander, pp. 118, pl. 1, fig. 3.

1989 *Craterisphaeridium sprucegrovense*, Cunha and Oliveira, pp. 302, pl. 1, fig. 10

2005 *Craterisphaeridium sprucegrovense* (Staplin), González et al., pp. 63, pl. 4, figs. 8, 9.

2013 *Puteoscorrum sprucegrovense* (Staplin, 1961), Wicander and Playford, pp. 610, pl. 4, figs. 7~9.

2015 *Craterisphaeridium sprucegrovense*, González et al., fig. 5E~G5.

描述膜壳原始呈球形至多边形,单壁,中空。膜壳表面具亚圆形至圆多边形凹穴。突起同型、坚硬、光滑,均匀分布于膜壳表面,可与膜壳自由连通。突起基部与膜壳接触区微扩大,向末端逐渐变细。突起末端具4~8节掌状分枝,分枝实心、同型、光滑、纤细、末端逐渐变细且易弯曲(in English : Vesicle originally spherical to polyhedral, single walled, and hollow. The surface of the vesicle wall is subcircular to rounded polygonal foveolate. Processes homomorphic, rigid, psilate and evenly distributed whose interiors communicate with the vesicle cavity. The processes have expanded bases that contacts angular to slightly curved, and taper distally. At each tip, process divides into 4 to 8 in number, homomorphic, psilate, slender, tapering, flexible, and solid branches).

尺寸(基于1个标本)膜壳直径约35.6 μm;总直径约56.6 μm;突起长度约21 μm。

对比和评论 *Ammonidium loriferum* 与 *Craterisphaeridium sprucegrovense* 形状十分相似,但前者膜壳表面呈瘤点状,后者呈凹穴状.González et al. (2015, figs. 5E~5G)的 *C. sprucegrovense* 非常像 *A. loriferum*,由于没有描述,很难进一步判断该种属于 *A. loriferum* 或 *A. sprucegrovense*. 报道于伊比利亚半岛西南部被错误拼写的“*C. sprucegrovenses*”(应为 *C. sprucegrovense*)标本(Pereira et al., 2018, figs. 8, 4)既无瘤状纹饰,也无凹穴状纹饰,本文认为该标本不属于 *A. sprucegrovense*. *Puteoscorrum polyankistrum* Wicander and Loeblich(1977)与 *Puteoscorrum sprucegrovense* (Staplin, 1961), Wicander and Playford(2013)外形十分相似,区别在于前者突起末端的二级分枝尾部具有再次分枝结构,本文将

*Puteoscortum polyankistrum* 视为 *Ammonidium sprucegrovense* 的变种, 即 *Ammonidium sprucegrovense* var. *polyankistrum* Wicander and Loeblich (1977). *Baltisphaeridium paleozoicum* (Stockmans and Willière, 1962b, p. 56, pl. 1, fig. 12; fig. 13) 与 *Baltisphaeridium microfurcatum* (Stockmans and Willière, 1962a, p. 92—93, pl. 2, figs. 18~20; fig. 12) 仅有素描图及不太清楚的标本图片, 并且在描述中不曾介绍膜壳表面是否具有瘤点或者凹穴, 本文对这两个种并入该种保留意见.

产地与时代西班牙西南部弗拉阶上部—法门阶(González et al., 2005, 2015); 加拿大西部弗拉阶(Staplin, 1961; Turner, 1986); 比利时弗拉阶中部—法门阶下部(Martin, 1981, 1982; Kimpe et al., 1978; Stockmans and Willière, 1962a, b, 1969, 1974); 葡萄牙法门阶(Cunhá and Oliveira, 1989); 美国 Illinois 和 Indiana 州法门阶(Wicander and Loeblich, 1977; Wicander and Playford, 2013); 新疆西准噶尔法门阶.

#### *Ammonidium levigatum* n. sp.

图版 1, 1~12

1983 *Hercyniana sprucegrovensis* var. *Sprucegrovensis*, Vangestaine et al., pp. 129, pl. 1, fig. 11.

2005 *Craterisphaeridium sprucegrovense* (Staplin) Turner, González et al., pp. 63, pl. 4, fig. 7, 10.

2007 *Ammonidiumloriferum*, Ghavidel-syooki and Owens, pp. 140, pl. 4, fig. 4.

2021 *Ammonidiumloriferum*, Stachacz et al., pp. 734, fig. 9, r.

全模图版 1, 图 8, 标本号: GNR62-4. 选模: 图版 1, 图 2, GNR58-2.

描述膜壳呈圆形或椭圆形, 外壁光滑, 单壁; 突起数量约 6~14, 均匀分布, 坚硬; 突起长约 11~21  $\mu\text{m}$ , 基部宽约 3~5  $\mu\text{m}$ , 远端逐渐变细. 突起末端具有二级掌状分枝结构, 分枝数量约 4~7, 等长或近等长, 易弯曲. 突起通常具有同型性, 可与膜壳相连通, 突起末端分枝长约 4~6.5  $\mu\text{m}$  (in English: Vesicle wall spherical to ellipsoidal, laevigate, and single-walled; processes moderately numerous (usually 6 to 14), evenly spaced, and rigid; the processes 11 to 21  $\mu\text{m}$  in length, 3 to 5  $\mu\text{m}$  in diameter at base, ta-

pering distally, whose distal extremity divided into only one order of branching. The distal branching is divided into a cluster of 4 to 7 palmately, equal or near-equal length, flexible, and recurved filaments. The processes are usually homomorphic and can communicate freely with the vesicle interior (cavity), tips developed palmate pinnae (4 to 6.5  $\mu\text{m}$  in length).

大小(基于 12 个标本): 膜壳直径: 23.5  $\mu\text{m}$  (32.33  $\mu\text{m}$ ) 35.9  $\mu\text{m}$ ; 突起长度: 11.2  $\mu\text{m}$  (14.7  $\mu\text{m}$ ) 21.85  $\mu\text{m}$ ; 突起基部宽度: 1.7  $\mu\text{m}$  (3.5  $\mu\text{m}$ ) 11  $\mu\text{m}$ ; 分枝长度: 4.3  $\mu\text{m}$  (5.2  $\mu\text{m}$ ) 6.5  $\mu\text{m}$ .

名字来源来源于拉丁语 *levigatus*, 表示“光滑的”.

对比和评价 *Ammonidium levigatum* n. sp. 的形状与 *A. sprucegrovense* 和 *A. loriferum* 极其相似. 不同点在于膜壳表面的纹饰, 前者为光滑表面, 后两者分别为凹穴状和瘤点状. 报道于伊朗东北部的“*Ammonidiumloriferum*”(Ghavidel-Syooki and Owens, 2007, plate 4, fig. 4)似乎具有光滑表面, 因此可能属于 *Ammonidium levigatum* n. sp.. 报道于新疆北部布龙果尔剖面的“*Ammonidiumloriferum*”(Stachacz et al., 2021, fig. 9, r)也具有光滑的外表, 也应属于 *Ammonidium levigatum* n. sp.. González et al. (2005)报道了伊比利亚半岛的 *Craterisphaeridium sprucegrovense* (Staplin) Turner (1986), 其中图版 4, 图 7~10 中的图 7 和 10 与图 8 和 9 明显不同, 除了个体差异外, 图 8~9 膜壳表面具有明显地亚圆形至圆形孔穴(foveolae). 因此, 图 7 和 10 与 8~9 并非同种, 前两者更倾向属于新建的 *A. levigatum* n. sp.. 无独有偶, 尽管图片并不清晰, 但产自比利时和荷兰弗拉阶上部—法门阶下部的标本 *Hercyniana sprucegrovensis* 及 *Hercyniana sprucegrovensis* var. *sprucegrovensis*(见 Kimpe et al., 1978, pl. 13, figs. 5, 6; Vangestaine et al., 1983, pl. 1, fig. 11)并没有像该模式种描述的凹穴状表面, 因此该标本很可能属于 *Ammonidium levigatum* n. sp.. 除此以外, 前人所报道的部分曾归于 *A. loriferum* 及 *A. sprucegrovense* 及其同义名的部分标本也可能属于 *Ammonidium levigatum* n. sp..

产地与时代伊比利亚半岛西南部法门阶(Pereira et al., 2018; González et al., 2005 pp. 63, pl. 4, figs. 7~8); 伊朗东北部法门阶(Ghavidel-

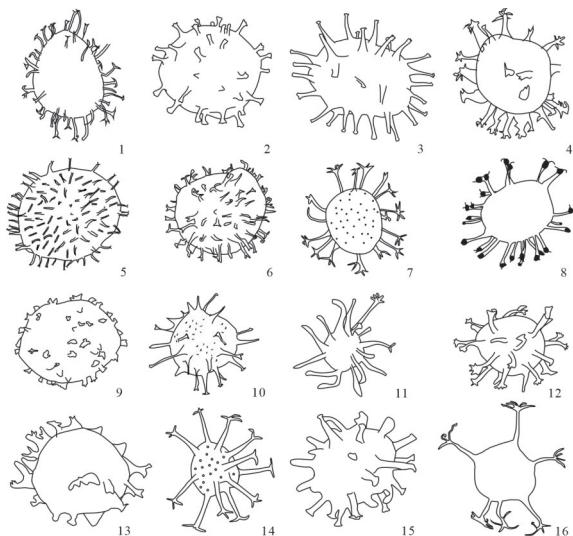
图3 *Ammonidium*属部分重要种素描图

Fig. 3 Idealized line drawings of selected *Ammonidium* species described from literature

1. *Ammonidium grosjeani*(Stockmans and Williere, 1962a) Martin (1981);2. *A. alloiteaui*(Deunff, 1955) Martin, (1981);3. *A. waldronense*(Tappan and Loeblich, 1971) Dorning(1981);4. *A. multipugiunculatum*(Cramer and Díez, 1977)Rubinstein(in Rubinstein *et al.*, 1999);5. *A. lewisi* Lister(1970);6. *A. aduncum* Playford and Martin(1984);7. *A. loriferum*(Deunff) Hashemi and Playford(1998);8. *A. maravillosum*(Cramer, 1969) Thusu;9. *A. furtivum* Playford and Martin(1984);10. *A. microcladum*(Downie, 1963) Lister(1970);11. *A. iowaensis* Wicander and Wood(1997);12. *A. uncinum* Loeblich and Wicander (1976);13. *A. conicum* Pôthe de Baldis(1998);14. *A. sprucegrovense* Martin(1981);15. *A. cornutum* Loeblich and Wicander(1976);16. *A. levigatum* n. sp.

Syooki and Owens, 2007, plate 4, fig. 4)和新疆北部法门阶(Stachacz *et al.*, 2021, fig. 9r).

## 4 *Ammonidium*属及其相关种的生物地层及古地理分布

### 4.1 生物地层

生物地层在确定生物化石的时空分布、地层形成和发育规律以及确定地层的相对地质年代方面具有重要的作用(如:文茭等,2020)*Ammonidium*相关种在文献中的地层分布见图4.从文献概述及生物分类修订来看,*Ammonidium*最早的种是出现于上寒武统(芙蓉统?)的*Multiplicisphaeridium canadense* Staplin,本文将该种归为*Ammonidium*,是因为其分枝仅现于突起的末端.该属繁盛于志留纪,最晚出现于密西西比亚纪(Mississippian,石炭纪).奥陶纪*Ammonidium*有13个种被包含在内,主

要有 *A. multipugiunculatum*, *A. furcatum* comb. nov., *A. macilentum*, *A. furtivum*, *A. raplaense* comb. nov., *A. parvipinnatum* comb. nov., *A. aduncum*, *A. acaciaense*, *A. bifurcatum* comb. nov., *A. belmontiforme*, *A. olsztymense*, *A. lichenoides* comb. nov., 及 *A. parvispinosum* comb. nov..其中,*A. parvipinnatum* comb. nov. 和 *A. aduncum*可延伸至志留纪(Llandovery to Wenlock)。这些种主要分布于撒哈拉一带(Deunff, 1961, 1964; Cramer and Díez, 1977)、哥伦比亚 Llanos 盆地(Rubinstein *et al.*, 2021)、伊朗(Ghavidel-Syooki, 2006)、澳大利亚西部 Canning Basin(Playford and Martin, 1984)、爱沙尼亚(Uutela and Tynni, 1991)、阿根廷(Ottone *et al.*, 1992)、丹麦 Bornholm(Smelror, 1987)、芬兰(Uutela, 1998)和波兰(Górka, 1979)。

志留纪是*Ammonidium*报道最多的时期,因此,前人将*Ammonidium*视为志留纪的典型属(Jachowicz, 2000).其中9个种可从兰多维列统(Llandovery)延伸至罗德洛统(Ludlow),主要有报道于美国 Ohio, Kentucky 和 Indiana 的 *A. micropilaris* comb. nov. 和 *A. encantador* comb. nov. (Cramer and Díez, 1972); 报道于北美及沙特阿拉伯的 *A. palmitella* (Cramer and Díez, 1972; Le Hérisse *et al.*, 1995); 报道于瑞典、英格兰、西班牙及北美的 *A. oligofurcatum* comb. nov. (Eisenack *et al.*, 1973); 报道于英格兰(Downie, 1963)、爱尔兰(Higgs and Williams, 2011)、立陶宛(Jankauskas and Gritytë, 2004)、约旦(Keegan *et al.*, 1990)、沙特阿拉伯(Le Hérisse *et al.*, 1995)、丹麦(Smelror, 1989)、加拿大(Eley and Legault, 1992)、瑞典(Eriksson and Hagenfeldt, 1997; Calner *et al.*, 2006)、阿根廷(García-Muro and Rubinstein, 2015)和巴拉圭(Gray *et al.*, 1992)的 *A. microcladum*; 报道于瑞典哥特兰岛的(Eisenack, 1954)、美国 Kentucky, Ohio, Indiana, Georgia(Cramer, 1970)及英格兰(Downie, 1963; Lister, 1970; Dorning, 1981)、阿根廷(de Inunciaga and Gutiérrez, 2011),及土耳其(Lakova and Göncüoğlu, 2005)的 *A. ludoviense*; 报道于瑞典(Schultz, 1967)的 *A. pustulatum* comb. nov., 和报道于瑞典哥特兰岛、西班牙、北美、弗洛里达、利比亚、突尼斯、比利时和英格兰的 *A. piriferum gotlandicum* comb. nov. 与 *A. piriferum*

*piriferum* comb. nov. (见 Eisenack *et al.*, 1973, p. 739).

有3个种报道于温洛克统(Wenlock),分别是报道于美国 Kentucky 州的 *A. ? pequenhum* (Cramer and Diez, 1972),美国 Indiana 州的 *A. waldronense* (Tappan and Loeblich, 1971) 和哈萨克斯坦的 *A. crinitum* (Grishina in Grishina and Klenina, 1981)。

罗德洛统至/或普里道利统(Pridoli)的代表种有奥地利的 *A. kahleri* comb. nov. (Bachmann and Schmid, 1964);阿尔及利亚撒哈拉(Jardiné and Yapaudjian, 1968)、利比亚(Cramer, 1970)、西班牙及美国 Florida (Cramer, 1970; Cramer and Díez, 1972) 的 *A. jardineae* comb. nov.;西班牙西北部(Cramer, 1970)的 *A. estrellaferum* comb. nov.;美国 Pennsylvania, Ohio, Indiana 和 Kentucky 的 *A. maravillosum* (Cramer, 1970; Cramer and Díez, 1972). 英格兰(Lister, 1970)的 *A. ? variabile*;阿根廷(Póthe de Baldis, 1998)及秘鲁(Vavrdová and Svobodová, 2010)的 *A. conicum*;美国 Oklahoma 州、秘鲁(Vavrdová and Svobodová, 2010)与阿根廷

(Muro *et al.*, 2018)的 *A. cornutum*;西班牙(Cramer, 1970)的 *A. belmonte*;西班牙(Cramer, 1970)、阿尔及利亚(Jardiné and Yapaudjian, 1968),利比亚(Cramer, 1970)及美国 Oklahoma (Loeblich and Tappan, 1970)的 *A. bonitum* comb. nov..

泥盆纪有17个种被报道,除了本文上述所提及的 *A. loriferum*, *A. sprucegrovense* 和 *A. levigatum* n. sp. 以外,还包括美国 Oklahoma(Loeblich and Tappan, 1970)的 *A. uncinum*,西班牙的 *A. carrascum* (Cramer, 1966),法国的 *A. exoticum* (Deunff, 1965a),加拿大和比利时的 *A. alloiteaui* (Deunff, 1955; Martin, 1981),美国 Iowa 州的 *A. iowaensis* (Wicander and Wood, 1997) 及澳大利亚西部的 *A. inornatum* (Colbath, 1990). 其余的种主要报道于上泥盆统,包括比利时和新疆北部的 *A. grosjeani* (Stockmans and Willière, 1962a; Lu and Wicander, 1988),美国 Ohio 州的 *A. hamatum*、*A. plenilunium* comb. nov. (Wicander, 1974),加拿大的 *A. truncatum* (Staplin, 1961) 和 *A. dispar* comb. nov. (Turner, 1986),比利时的 *A. maritimum*、*A. williereae*

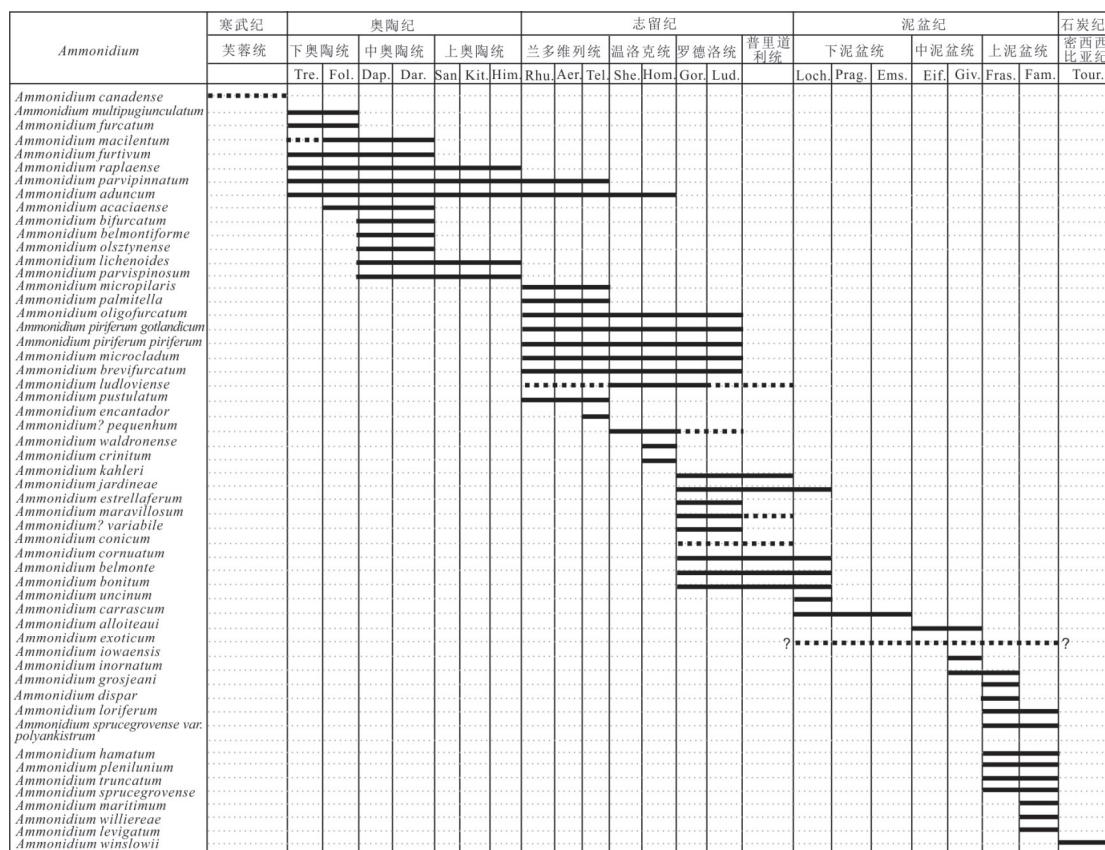


图4 文献中 *Ammonidium* 已知相关种的时代分布

Fig.4 Stratigraphical ranges of all known acritarchs of *Ammonidium* from the literature

comb. nov. (Martin, 1981; Martin, 1984). 值得一提的是, *A. winslowii* comb. nov. 最初属于 *Gorgonisphaeridium* Staplin, Jansonius and Pocock, 1965 属 (Staplin et al., 1965), 后被 Eisenack et al. (1973) 置于 *Multiplicisphaeridium*, 是极少数仅报道于石炭纪的种。

从图 5 可以看出, 3 个外形相似的种, 即 *A. loriferum*、*A. sprucegrovense* 和 *A. levigatum* n. sp. 主要报道于全球上泥盆统, 尤其是法门阶 (Staplin, 1961; Deunff, 1965b; Wicander and Loeblich, 1977; Martin, 1981; Lu and Wicander, 1988; Cunha and Oliveira, 1989; Hashemi and Playford, 1998; Ghavidel-Syooki, 2001; Filipiak, 2005; González et al., 2005; Ghavidel-Syooki and Owens, 2007; de Andrade et al., 2020; Wicander and Playford, 2013). *A. loriferum* 在欧美大陆 (Laurussia)、西冈瓦纳 (West Gondwana)、东冈瓦纳 (East Gondwana) 及哈萨克斯坦板块 (Kazakhstan Plate) 均有出现, 该种最早报道于西冈瓦纳中泥盆统的吉维特阶, 并在西冈瓦纳大陆延伸至法门阶, 在欧美大陆延伸至石炭系密西西比系。*A. sprucegrovense* 在欧美大陆、东冈瓦纳大陆和哈萨克斯坦板块也均有报道, 虽最早

出现于弗拉阶, 但主要报道于法门阶。*A. levigatum* n. sp. 则主要出现于法门阶, 因此, 该种可能是识别法门阶的重要标志性分子。

#### 4.2 古地理分布

关于有机质壳壁的海生微体浮游植物古地理及古生态分布的模型已有很多 (如: Le Hérisse et al., 1997, 2000; Li and Servais, 2002; Servais et al., 2003; Molyneux et al., 2013). Molyneux et al. (2013) 对早—中古生代 (寒武纪—泥盆纪) 疑源类的古地理作了总结, 早期认为疑源类古地理分布仅与古纬度和气候有关联, 但后来发现早期的古地理图与后来新的古地理图并非完全相同, 发现控制疑源类古地理分布的因素是古纬度、古温度、洋流、海陆分布格局、沉积环境和距海岸线远近等一系列因素共同作用的结果 (Molyneux et al., 2013). Cramer and Diez (1974) 尝试了较早的疑源类古地理分区, 将奥陶纪疑源类古地理划分为 “African Palynological Unit” 和 “American Palynological Unit”. 多数学者将 Vavrdová (1974) 的欧洲早奥陶世疑源类古地理研究作为疑源类生物古地理研究的起点, Vavrdová 将该时段的疑源类古地理分为 “Mediterranean Province” 和 “Baltica Province (或 Boreal Province)”

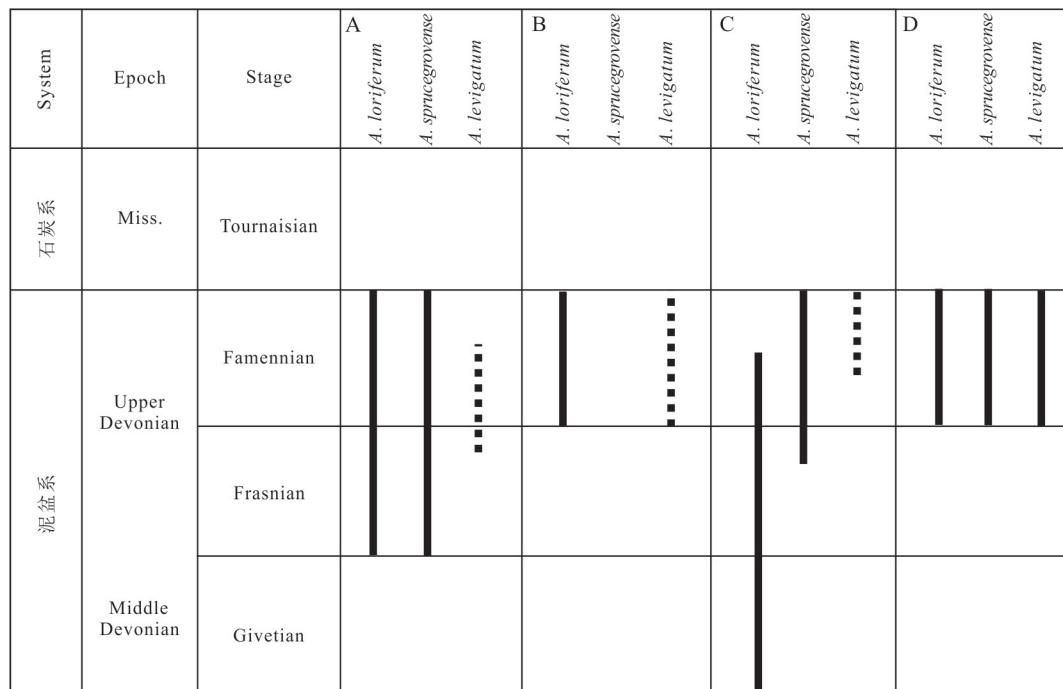


图 5 *A. loriferum*、*A. sprucegrovense* 和 *A. levigatum* n. sp. 3 个种在 4 个主要古地理单元的时代分布

Fig.5 Stratigraphical distribution of *A. loriferum*, *A. sprucegrovense*, and *A. levigatum* n. sp. discussed here in the four main palaeogeographical domains

A:劳亚大陆; B:东冈瓦纳; C:西冈瓦纳; D:哈萨克斯坦板块

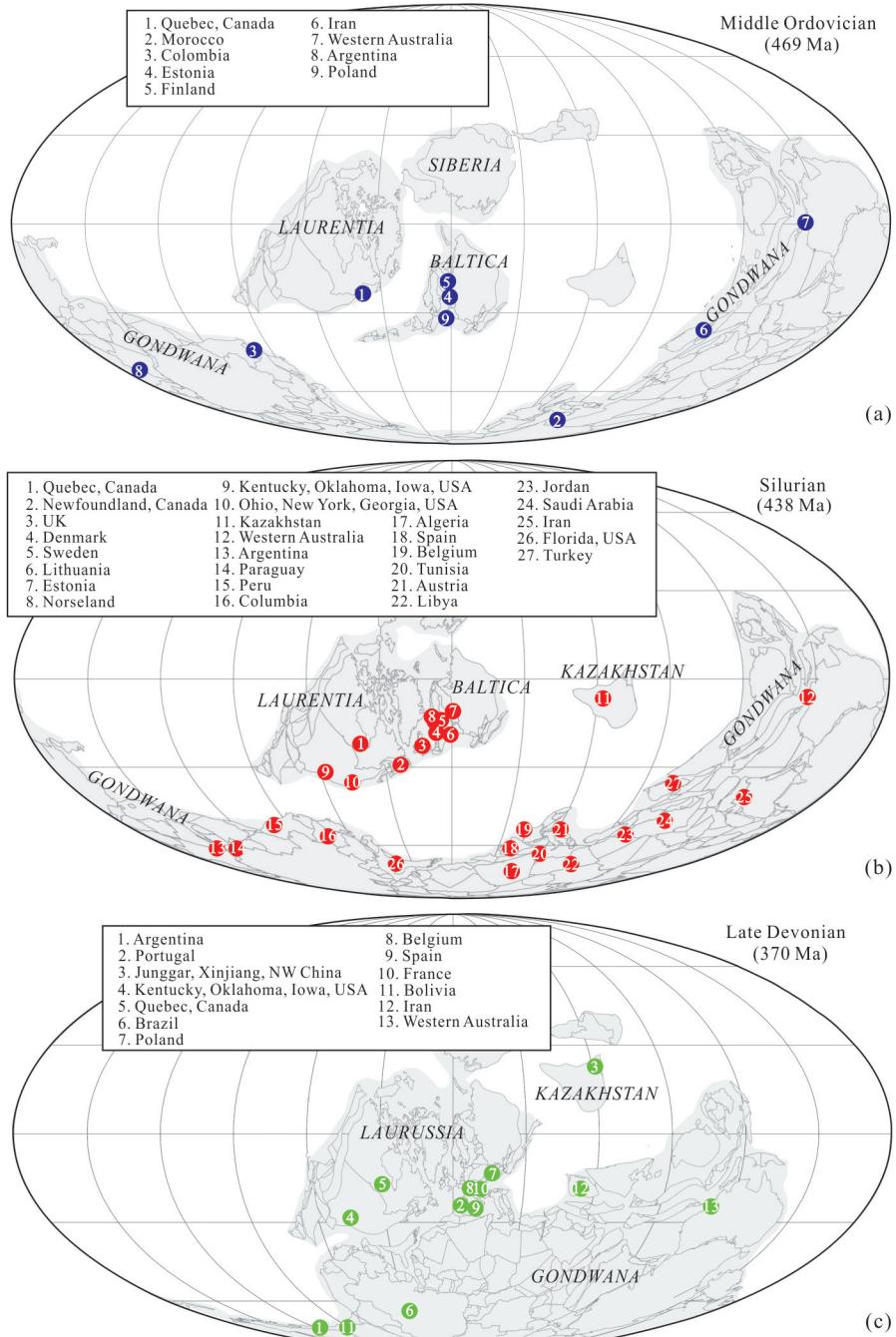


图 6 *Ammonidium* 在中奥陶世(a)、志留纪(b)和晚泥盆世(c)古地理复原图中的分布

Fig. 6 Palaeobiogeographical distribution of the *Ammonidium*-bearing assemblages on palaeogeographical reconstructions of the Middle Ordovician (a), the Silurian (b) and Late Devonian (c)

古地理图修改自 Boucot *et al.* (2013)

两个分区，前者包含比利时、法国、西班牙、北非、德国南部、波西米亚和保加利亚，后者包括俄罗斯北部、波兰、瑞典和德国北部。后来，“Perigondwana Province”取代“Mediterranean Province”逐渐被学者们广泛使用，Perigondwana Province 包括了冈瓦纳大陆边缘的非洲北部地区、欧洲南部地区、中东、巴

基斯坦、Avalonia(纽芬兰、爱尔兰、比利时、南威尔士、英格兰西北部等)、华南和阿根廷西北部部分地区，成为与“Baltica Province”共存的古地理分区 (Molyneux *et al.*, 2013)。采用定量方法，晚泥盆世疑源类古地理分区可划分为 3 个域，即东冈瓦纳域、西冈瓦纳域和北方域(Shen *et al.*, 2019)。

图6显示的是*Ammonidium*分别在中奥陶世( $\sim 469$  Ma)、志留纪( $\sim 438$  Ma)及泥盆纪( $\sim 370$  Ma)古地理复原图中的分布。奥陶纪*Ammonidium*总体呈全球分布,但分布较为有限,主要报道于加拿大、撒哈拉地区、澳大利亚西部、爱沙尼亚、波兰、芬兰、摩洛哥和阿根廷等劳伦大陆、波罗的大陆、东冈瓦纳和西冈瓦纳地区。志留纪是该属最繁盛的发展时期,超过25个地区具有相关属种的报道,具有全球广布特征。泥盆纪时期,该属的报道明显收缩,仅在劳亚大陆和冈瓦纳大陆边缘有分布。

## 5 结论

(1) *Ammonidium*是古生代常见的疑源类化石,在时代上,*Ammonidium*属最早报道于寒武纪晚期,繁盛于志留纪,并最终在密西西比亚纪(石炭纪)早期消失;在古地理上,*Ammonidium*在奥陶纪*Ammonidium*总体呈全球分布,但分布较为有限,主要报道于加拿大、撒哈拉地区、澳大利亚西部、爱沙尼亚、波兰、芬兰、摩洛哥和阿根廷等劳伦大陆、波罗的大陆、东冈瓦纳和西冈瓦纳地区。志留纪是该属最繁盛的发展时期,超过25个地区具有相关属种的报道。泥盆纪时期,该属的报道明显收缩,仅在劳亚大陆和冈瓦纳大陆边缘有分布。

(2) 将 *Caiacorymbifer* Tappan and Loeblich (1971), *Gracilisphaeridium* Eisenack and Cramer (1973), *Naevisphaeridium* Wicander (1974), *Puteosphaeridium* Deunff, 1981, *Pertusisphaeridium* Turner (1986) 和 *Martinsphaeridium* Sarjeant and Vavrdová (1997) 等相似属纳入*Ammonidium*属的晚出异名。*Ammonidium sprucegrovense* var. *polyankistrum* Wicander and Loeblich (1977)由种级降为了变种级。膜壳呈圆形/椭圆形,单壁,膜壳表面具纹饰(光滑、凹穴、瘤点等),突起末端具有二级分枝结构特征,且基部可与膜壳自由连通的标本可归为*Ammonidium*。

(3) 过去一些被鉴定为*A. loriferum*与*A. sprucegrovense*及其晚出异名的标本应属于新建立的*A. levigatum* n. sp.,该种是晚泥盆世的特征种,尤其在法门期具有全球性分布特征,可作为识别上泥盆统的标准化石。

致谢:由于部分早期外文文献无法逐一获取,引用和列举前人成果受到限制,谨向领域内所有作

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