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A STUDY ON ONTOGENY AND EVOLUTION OF ROBUSTOSCHWAGERINIDS (PERMIAN FUSULINIDS)

Yang Xiang-ning* and Hao Yi-chun

(China University of Geosciences, Beijing)

Summary

Based on large amount of specimens and data gathered from literature, a detailed morphometric analysis has been conducted to study the ontogeny and evolution of robustoschwagerinids, a group of Permian Schwagerinidae including 31 species originally put under the name of *Robustoschwagerina* M.-Maclay, 1956 (Table I).

For all the species studied, the rate of shape change has been calculated and compared for each volution, which was defined as the ratio of the non-overlap area between two adjacent volutions to the area of preceding volution (Fig. 1). Three different types of shape change, labeled as A, B and C respectively in the inset of Figure 1, have been recognized in the ontogenetic process of robustoschwagerinids.

This morphometric study has revealed that the ontogenetic process of robustoschwagerinids may be divided into three stages. The juvenile stage is characterized by high rates of shape change and allometric growth; the pre-adult stage is relatively short and usually represented by only one volution, while the adult stage is characterized by low rates of shape change and isometric growth.

The most important morphological changes in the ontogeny of robustoschwagerinids all occurred in the pre-adult stage, i.e., in a short period when the juvenile organism was developed into maturity, such as the reduction or disappearance of the chomata, the abrupt inflation of the test, the rapid decrease in the relative thickness of spirotheca, etc. Two patterns of shape change have been recognized in robustoschwagerinids when the organisms were developed from juvenile to adult. In some species, such as *R. tumidiformis*, *R. kahleri*, *R. guangnanica*, *R. brevaxiformis*, etc., the shape of adult tests appeared gradually and the shape of pre-adult volution showed a transitional character from juvenile to adult tests. In other species, such as *R. hidensis*, *R. magna*, *R. yunnanensis*, *R. longlinensis*, *R. changmeensis* and *R. ziyunensis*, the shape of adult tests seemed to have been formed suddenly without any transition from juvenile to adult, though a pre-adult volution also could be identified.

Accompanying the morphological changes was the change in the mode of life of organism during the ontogenetic process. From the viewpoint of functional morphology, the juvenile individuals of robustoschwagerinids with a fusiform test and heavy chomata were obviously adaptable to a benthic life, while the adult individuals with a highly inflated spherical test were probably adaptable to a floating life. A comparison between the statistic distributions of the relative thickness of

* Current address: Department of Earth Sciences, Nanjing University, Nanjing 210008, China.

spirotheca (defined here as the ratio of the thickness of spirotheca to the width of the volution) in the juvenile and adult tests of robustoschwagerinids and in *Triticites* has shown the remarkable similarity between the juvenile shells of robustoschwagerinids and *Triticites*. However, the distribution of relative thickness of spirotheca in the adult tests of robustoschwagerinids is apparently different from those in both the juvenile shells and *Triticites*, indicating the different adaptive nature of the adult tests. These provide further evidence to support the idea that robustoschwagerinids had a benthic habit in juvenile period and a floating habit in adult period.

Although the juvenarium of *Robustoschwagerina* has long been described as “*Triticites*-like”, detailed studies suggested that the species of *Robustoschwagerina*, except *R. nucleolata* (Ciry), could be divided into two groups with juvenarium in different forms. The first group includes such species as *R. tumida*, *R. tumidiformis*, *R. kahleri*, *R. subsphaerica*, etc., with a juvenarium consisting of 1 to 3 volutions and similar to the test of young *Triticites* (Pl. II, figs. 10—17), which is termed the “juvenile *Triticites*-like”, juvenarium in this paper. The second group includes such species as *R. longlinensis*, *R. spatiosa*, *R. magna*, *R. yunnanensis*, etc., with a juvenarium composed of at least 4 tightly coiled volutions and similar to the test of adult *Triticites*, which will be described as the “adult *Triticites*-like” juvenarium (Pl. II, figs. 18—29) in this paper.

The similarities in morphology and habit between the juvenile shell of robustoschwagerinids and *Triticites* suggest that *Triticites* was the common ancestor of robustoschwagerinids. However, the evolutionary changes leading to the formation of various robustoschwagerinid species happened in different stages of the ancestral ontogeny. Heterochronic explanations have been proposed for the origin and evolution of different species groups of robustoschwagerinids. In the species with an “adult *Triticites*-like” juvenarium, the evolutionary changes apparently occurred in the later stage of the ancestral ontogeny and were related to peramorphism (sensus McNamara, 1986). In the species with a “juvenile *Triticites*-like” juvenarium, these changes occurred in the early stage of the ancestral ontogeny and were probably associated with the peramorphism and acceleration.

The earliest robustoschwagerinids fauna has been found from the *Pseudoschwagerina morsei*-*Robustoschwagerina xiaodushanica* Zone of the Maping stage in the Xiaodushan section, Babao, Yunnan and from the *Pseudoschwagerina cheni* Subzone in the Malaoshan section, Yishan, Guangxi; it is characterized by the sudden appearance of many different species (Text-fig. 7; Tab. II). The authors believe that the rapid origination and evolutionary radiation of robustoschwagerinids were closely related to their floating habit in adult stage which permitted the animals to intrude into a new ecological space previously unexploited by fusulinids.

Based on the ontogenetic and morphological features, the classification of robustoschwagerinids can be proposed as follows:

1). *Robustoschwagerina* (*Robustoschwagerinoides*) Sheng, Wang et Zhong, 1984 (type species: *Pseudoschwagerina nucleolata* City, 1945) may be regarded as an independent genus, since this species group has an indistinct, spherical juvenarium which makes it different from other groups.

2). The genus *Robustoschwagerina* M.-Maclay, 1956 should be restricted to those species represented by *R. tumida*, *R. tumidiformis*, etc. with a “juvenile *Triticites*-like” juvenarium.

3). Some species of robustoschwagerinids found in southwestern China, such as *Robustoschwagerina longlinensis* Dong, 1984, etc., are characterized by their “adult *Triticites*-like” juvenarium and can be distinguished from the typical species of *Robustoschwagerina*. A new genus, *Longlinia* gen. nov. with *Robustoschwagerina longlinensis* Dong, 1984 as the type species, has been established for this species group. Besides the type species, the new genus also includes *Robustoschwagerina spatiosa* Lin, 1979, *R. magna* Zhang et Dong, 1986, *R. ziyunensis* Zhang et Dong, 1986, *R. bianpinensis* Zhang et Dong, 1986, *R. yunnanensis* Sheng, Wang et Zhong, 1984 and *R. changmeensis* Xia et Dong, 1986.

DESCRIPTION OF NEW SPECIES

Genus *Robustoschwagerinoides* Sheng, Wang et Zhong, 1984

Type species *Pseudoschwagerina nucleolata* Ciry, 1943

Diagnosis Test spherical or subspherical, loosely coiled; juvenarium spherical and indistinct, consisting of 1—1.5 volutions; spirotheca thin; septa unfluted; chomata weak or absent; proloculus large.

Remarks This genus differs from *Robustoschwagerina* in its spherical juvenarium. It also differs from *Zellia* which has thicker spirotheca and septa, and more septal pores.

Robustoschwagerinoides minutalis sp. nov.

(Pl. III, figs. 7, 8)

Diagnosis Test medium, subspherical, composed of 5—6.5 volutions, 3.2—3.7 mm long and 4.1—4.4 mm high, with a form ratio of about 0.71—0.86:1. Juvenarium spherical, consisting of 1—1.5 volutions. Spirotheca thickening gradually from inner to outer whorls. Septa flat. Chomata weak, developed in the first three volutions.

Remarks The new species is distinguishable from *Robustoschwagerinoides nucleolata*(Ciry) by its spherical test, smaller size and form ratio.

Horizon and locality Maping stage, Babao, Yunnan.

Robustoschwagerinoides simplex sp. nov.

(Pl. II, figs. 10—12)

Diagnosis Test medium to large, spherical, slightly umblicated at both poles, consisting of 4—6 whorls; 6.5—8.5 mm long and 5.3—7.3 mm high, with a form ratio of about 0.7—0.8:1. Juvenarium spherical or subspherical, composed of only one volution. Spirotheca thin. Septa flat. Chomata small, existing only in the first two volutions. Proloculus large, spherical.

Remarks This species is similar to *Robustoschwagerinoides minutalis* sp. nov. described above, but it can be distinguished from the latter by the larger and umblicated test when the number of volutions in both species is the same.

Horizon and locality Maping stage, Babao, Yunnan.

Genus *Robustoschwagerina* M.-Maclay, 1956

Type species *Schwagerina tumida* Licharev, 1934

Diagnosis Test large, spherical to subspherical; juvenarium “juvenile *Triticites*-like”, consisting of 1—3 fusiform whorls; septa slightly fluted in the juvenarium, and flat in the adult; chomata well developed in the juvenarium, but weak or absent in the adult; proloculus large, spherical.

Remarks By the distinct fusiform juvenarium, *Robustoschwagerina* M.-Maclay, 1956 can be easily distinguished from *Robustoschwagerinoides* Sheng, Wang et Zhong, 1984.

Robustoschwagerina obesa sp. nov.

(Pl. III, figs. 5, 6, 9)

Diagnosis Test medium, subspherical, composed of 6—7 whorls; 3.7—4 mm long and 5.1—

5.6 mm high, with a form ratio of about 0.7—0.8:1. Juvenarium “juvenile *Triticites*-like”, consisting of 2—3 volutions; first volution subspherical, while second and third ones inflated-fusiform, with a form ratio of 1.4—1.6:1. Septa unfluted. Chomata existing only in the juvenarium, and absent in the outer whorls. Proloculus spherical.

Remarks The new species seems to resemble *Robustoschwagerina kahleri* (M.-Maclay), 1949, but in the former, the test is smaller, and the juvenarium has more volutions with a large form ratio.

Horizon and locality Maping stage, Babao, Yunnan.

Robustoschwagerina yishanensis sp. nov.

(Pl. II, fig. 7)

Diagnosis Test medium, spherical, composed of 7—7.5 whorls; 5.1—5.2 mm long and 4.7—5.1 mm high, with a form ratio of about 1—1.1:1. Juvenarium “juvenile *Triticites*-like”, consisting of 3 volutions, with a form ratio of about 2.2:1. Shape of fourth whorl showing a transitional character from juvenarium to adult test. Chomata well developed in the juvenarium but absent in the outer whorls. Septa slightly fluted in the juvenarium. Proloculus spherical.

Remarks The new species is similar to *Robustoschwagerina guangnanica* Sheng, Wang et Zhong, 1984 in the juvenarium, but in the latter, the test is subspherical, with a form ratio smaller than 0.9:1, while in the former, the test is spherical, with a form ratio of about 1—1.1:1.

Horizon and locality Maping stage, Yishan, Guangxi.

Robustoschwagerina guangxiensis sp. nov.

(Pl. II, figs. 5, 6)

Diagnosis Test medium, subspherical, consisting of 5—6.5 volutions; 5.1—5.9 mm long, 4.3—4.9 mm high; form ratio about 1.2:1. Juvenarium “juvenile *Triticites*-like”, fluted-fusiform, composed of 1.5—2 volutions, with a form ratio of 1.8—1.9:1. Chomata existing only in the juvenarium. Septa slightly fluted in the first two whorls and flat in the outer whorls. Proloculus large, spherical.

Remarks The new species is similar to *Robustoschwagerina xiaodushanica* Sheng, Wang et Zhong, 1984 in the outline of the test, but differs in the juvenarium which has a form ratio of 1.8—1.9:1 in the former, but larger than 2.1:1 in the latter.

Horizon and locality Maping stage, Yishan, Guangxi.

Genus *Longlinia* gen. nov.

Type species *Robustoschwagerina longlinensis* Dong, 1984

Diagnosis Test medium to large, spherical or subspherical; juvenarium “adult *Triticites*-like”, composed of 4—6 tightly coiled volutions; septa fluted in the juvenarium and flat in the outer whorls; chomata well developed in the juvenarium, but becoming weak or absent in the adult; proloculus spherical, medium to large in size.

Remarks The new genus differs from *Robustoschwagerina* in the “adult *Triticites*-like” juvenarium composed of at least 4 volutions, which is “juvenile *Triticites*-like” and comprises 1—3 volutions in the latter.

***Longlinia densa* gen. et sp. nov.**

(Pl. II, figs. 8, 9)

Diagnosis Test medium, subspherical, consisting of 8—9 volutions, 5.5 mm long and 4.4—4.9 mm high, with a form ratio of about 1.1—1.2:1. Juvenarium typically “adult *Triticites*-like”, composed of 4—5 tightly coiled whorls, with a form ratio of about 2.5:1. Spirotheca gradually thickening outwards. Septa slightly fluted only in the first 5 whorls. Chomata well developed in the juvenarium, becoming weak in the outer whorls. Proloculus spherical, small-sized.

Remarks The species is the smallest among the species with an “adult *Triticites*-like” juvenarium.

Horizon and locality Maping stage, Yishan, Guangxi.

图 版 说 明

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图 版 I**1,2. *Robustoschwagerina tumida* (Licharev)**

1.轴切面。2.轴切面,最外圈部分保存不全。均×6。登记号:RO-001,RO-002。陕西镇安石门垭剖面,*Robustoschwagerina-Zellia* 带。

3,4. *Robustoschwagerina tumidiformis* (A. D. M.-Maclay)

3.轴切面。4.轴切面,最外圈部分保存不全。均×6。登记号:RO-003,RO-004。云南八宝小独山剖面。*Pseudoschwagerina parabeedei-Sphaeroschwagerina sphaerica* 带。

5,6. *Robustoschwagerina kahleri* (A. D. M.-Maclay)

轴切面。均×6。登记号:RO-005,RO-006。产地同上,*Pseudoschwagerina morsei-Robustoschwagerina xiaodushanica* 带。

7,8. *Robustoschwagerina yunnanensis* Sheng, Wang et Zhong

轴切面,均×6。登记号:RO-007,RO-008。产地同上,*Pseudoschwagerina robusta-Zellia chengkungensis* 带。

9,10. *Robustoschwagerina regularis* (Ciry)

9.轴切面,×6。登记号:RO-009。云南八宝小独山剖面,*Pseudoschwagerina morsei-Robustoschwagerina xiaodushanica* 带。

10.轴切面,×8。登记号:RO-010。广西宜山马脑山剖面,*Sphaeroschwagerina subrotunda-Robustoschwagerina* 亚带。

11,12. *Robustoschwagerina subsphaerica* (Nogami)

11.轴切面。12.轴切面,最外圈部分保存不全。均×6。登记号:RO-011,RO-012。陕西镇安石门垭剖面,*Robustoschwagerina-Zellia* 带。

图 版 II**1,2. *Robustoschwagerina pamirica* Leven et Scherbovich**

轴切面,均×8。登记号:RO-013,RO-014。广西宜山马脑山剖面,*Sphaeroschwagerina subrotunda-Robustoschwagerina* 亚带。

3. *Longlinia bianpingensis* (Zhang et Dong)

轴切面,×6。登记号:RO-015。云南八宝小独山剖面,*Pseudoschwagerina robusta-Zellia chengkungensis* 带。

4. *Robustoschwagerina minima* Zhang et Dong

轴切面,×8。登记号:RO-016。广西宜山马脑山剖面,*Sphaeroschwagerina subrotunda-Robustoschwagerina* 亚带。

5,6. *Robustoschwagerina guangxiensis* sp. nov.