

Article original

Morphometric analysis of Tremadocian (earliest Ordovician)
kirkocystid mitrates (Echinodermata, Stylophora)
from the Taebaeksan Basin, Korea

Analyse morphométrique de mitrates kirkocystides (Echinodermata,
Stylophora) du Trémadocien (Ordovicien inférieur)
du bassin de Taebaeksan, Corée

Seung-Bae Lee ^a, Bertrand Lefebvre ^{b,*}, Duck K. Choi ^a

^a Seoul national university, Seoul 151-747, Earth and environmental sciences, Korea

^b UMR Biogéosciences, université de Bourgogne, 6, boulevard Gabriel, 2100 Dijon, France

Received 21 January 2003; accepted 28 May 2003

Available online 27 October 2004

Abstract

Abundant isolated remains of stylophoran echinoderms (cornutes and mitrates) are reported for the first time in the late Tremadocian (*Asaphellus* Zone) Tumugol Formation of Korea. Mitrates include numerous adorals of Kirkocystidae. Several new important anatomical features have been observed on these adorals, as an internal calcitic layer that is associated to s_2 and possibly also to the palmar complex. This observation suggests that the palmar complex would be present not only in mitrocyttid mitrates, but also in peltocystitids. For the first time, several morphometric analyses have been undertaken based on isolated kirkocystid adorals, so as to explore the morphological diversity displayed by Korean adorals, but also in order to compare their morphology with that of other Gondwanan kirkocystids. Morphometric analyses indicate the occurrence of two contrasted morphologies within Korean adorals (morphotypes A and B), and of three distinct morphologies within European and North African forms (“*Anatifopsis*”, “*Balanocystites*”, and “*escandei*” morphotypes). Comparison of Korean adorals with those from Europe and North Africa shows that: (1) morphotypes B and “*Anatifopsis*” are equivalent; consequently, the two Korean specimens referred to morphotype B are assigned to the genus *Anatifopsis*; (2) morphology of most Korean adorals, which belong to morphotype A, is clearly distinct from that of all other described kirkocystids from Europe and North Africa. The small size, juvenile morphology, and great morphological variability observed in the morphotype A of the Korean adorals are suggestive of possible heterochronic processes (peramorphosis).

© 2004 Elsevier SAS. All rights reserved.

Résumé

Des restes abondants d'échinodermes stylophores (cornutes et mitrates) sont signalés pour la première fois dans la Formation de Tumugol, du Trémadocien supérieur (Zone à *Asaphellus*) de Corée. Les fragments de mitrates comprennent de nombreuses adorales de kirkocystidés. L'examen de ces adorales a permis de mettre en évidence diverses structures, parmi lesquelles un repli calcitique interne, associé à la fois à s_2 et vraisemblablement au complexe palmaire. Cette observation suggère que le complexe palmaire serait présent non seulement chez les mitrates mitrocystitides, mais également chez les peltocystides. Diverses analyses morphométriques sont réalisées, pour la première fois, sur des adorales isolées de kirkocystidés, dans le but d'explorer la diversité morphologique des spécimens de Corée, et de les comparer avec la plupart des formes gondwaniennes connues. Les analyses morphométriques mettent en évidence deux morphologies contrastées (morphotypes A et B) chez les formes de Corée, et trois morphologies distinctes au sein des adorales d'Europe et d'Afrique du Nord (morphotypes

* Corresponding author. Tel : +33-3-8039-3970; Fax : +33-3-8039-6387.

E-mail address: bertrand.lefebvre@u-bourgogne.fr (B. Lefebvre).

« *Anatifopsis* », « *Balanocystites* » et « *escandei* »). La comparaison des adorales de Corée avec celles d'Europe et d'Afrique du Nord montre que : (1) les morphotypes B et « *Anatifopsis* » sont équivalents ; par conséquent, les deux adorales coréennes appartenant au morphotype B sont rapportées au genre *Anatifopsis* ; (2) la morphologie des adorales de type A, qui rassemblent la grande majorité des spécimens coréens, est clairement différente de celle des adorales européennes et nord-africaines. La petite taille, la morphologie juvénile, et l'importante variabilité morphologique des adorales coréennes de type A suggèrent l'influence possible de processus hétérochroniques (péramorphose).
© 2004 Elsevier SAS. All rights reserved.

Keywords: Stylophorans; Echinoderms; Tremadocian; Korea; Morphometrics; Heterochronic processes

Mots clés : Stylophores ; Échinodermes ; Trémadocien ; Corée ; Morphométrie ; Processus hétérochroniques

1. Introduction

Very little has been published on Ordovician echinoderms from Korea (Kobayashi, 1934, 1960; Choi and Lee, 1988). The Lower Ordovician Tumugol and Mungok formations have yielded rich and diverse invertebrate faunas including trilobites, brachiopods, bivalves, gastropods, cephalopods, and conodonts, but also several echinoderm fragments, comprising isolated cystoid plates (Kobayashi, 1960) and stems assigned either to solutes or to cystoids (Kobayashi, 1934; Regnell, 1945; Spencer, 1950) or more likely to crinoids (Choi and Lee, 1988). A late Tremadocian age (*Asaphellus* Zone) for both the Tumugol and Mungok formations is suggested by the trilobite fauna (Kobayashi, 1934, 1960; Kim et al., 1991; Choi et al., 2001). However, aside from trilobites and conodonts, little attention has hitherto been paid to other fossil groups.

In this study, we report on stylophoran echinoderms from the upper Tremadocian Tumugol Formation of Korea. The Tumugol Formation has yielded numerous isolated skeletal elements that can be assigned to cothurnocystid cornutes and to peltocystid mitrates belonging to the family Kirkocystidae. Cornute remains will be described in a separate paper. The occurrence of the kirkocystid genus *Anatifopsis* in the Tremadocian of Korea had been previously reported. This fossil was assigned either to cirripeds (Kobayashi, 1960) or to problematica (Choi and Lee, 1988; Choi and Kim, 1989; Choi, 1990). The phyletic position of *Anatifopsis* has been controversial since its original description by Barrande (1872), because of its unusual, “bivalved” morphology resulting from the great expansion of two large skeletal elements (adorals), which cover both the whole upper and most of the lower surface of the animal. Internal moulds of isolated adorals of kirkocystids were erroneously interpreted as disarticulated valves of cirriped crustaceans and termed *Anatifopsis* by Barrande (1872); more complete, articulated specimens were assigned to the echinoderm genus *Balanocystites* by the same author (Barrande, 1887). Following Barrande (1872), internal moulds of kirkocystid adorals have been designated as *Anatifopsis* and variously interpreted as isolated valves of cirriped (Le Goarant de Tromelin and Lebesconte, 1876; Reed, 1907; Chauvel, 1941, 1966, 1981), phyllocarid (Hadding, 1913; Rolfe, 1969; Pillet and Beaulieu, 1998), and phyllopod (Thoral, 1935; Dean, 1966) crustaceans, but also as bivalves (Jones and Woodward, 1895) and

machaeridians (Withers, 1926). The possible echinoderm affinities of *Anatifopsis* have been first discussed and rejected by Chauvel (1941, 1981), who erected the echinoderm genera *Anatiferocystis* (1941) and *Guichenocarpos* (1981) for undisputable echinoderms exhibiting strong morphological similarities with the crustacean genus *Anatifopsis*. Following Pope (1975) who suggested a possible relationship between *Anatifopsis* and mitrates, Jefferies (1979, 1986) established that *Anatifopsis* corresponds to internal moulds of isolated adorals belonging to the two kirkocystid genera *Balanocystites* and *Anatiferocystis*. This interpretation is now widely accepted (Domínguez and Gutiérrez, 1990; Lefebvre, 1999, 2000a; Parsley et al., 2000).

Kobayashi (1960) first reported the occurrence of *Anatifopsis* in Korea based on several isolated adorals from the Mungok Formation (Tremadocian) of Yongwol area (Fig. 1). He distinguished two different species, *A. cocaban* and

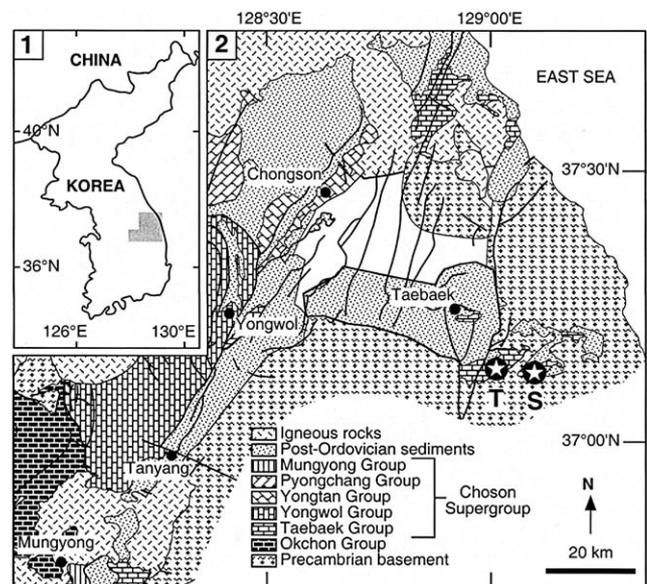


Fig. 1. Locality maps. 1. Map of Korean peninsula showing the position of study area. 2. Simplified geologic map showing the distribution of the Choson Supergroup in the Taebaek Basin, Korea. Circled stars in the lower right represent fossil localities, Tongjom (T) and Sokkaejae (S) sections.

Cartes de localisation des affleurements. 1. Carte de la péninsule coréenne indiquant la région d'étude. 2. Carte géologique simplifiée montrant la distribution du Super Groupe de Choson, bassin de Taebaeksan, Corée. Les deux étoiles représentent les coupes ayant fourni des restes de stylophores : Tongjom (T) et Sokkaejae (S).

A. truncata. The new material has been collected in the more or less contemporaneous stratigraphic interval (*Asaphellus* Zone) of the Tumugol Formation, Taebaek area (Fig. 1) and consists of more than 70 internal moulds of kirkocystid adorals. New specimens are small rectangular elements (2–10 mm long), displaying a great morphological variability. This variability raises the questions of the presence of several morphotypes in the Korean material, possibly related to the co-occurrence of different species or to a possible asymmetry between left and right adorals (as in some other kirkocystids). Another intriguing aspect of Korean isolated adorals is their extremely short and broad morphology, which clearly differs from that of most other kirkocystids, but recalls that observed in juvenile specimens belonging to other species. The small size of Korean adorals and their unusual, juvenile aspect are possibly indicative of heterochronic processes.

The aims of this study are (1) to document new anatomical features in internal moulds of kirkocystid adorals based on new specimens from the Tumugol Formation, (2) to investigate the great morphological variability occurring within Korean adorals, and (3) to compare their unusual morphology with that of all other previously described Gondwanan kirkocystids. As many times as possible, several ontogenetic stages (based on concentric growth lines) will be considered for each specimen, so as to test the possible influence of heterochronic processes.

1.1. Institutional abbreviations

CGSP: Czech Geological Survey, Prague

FSL : Université Claude Bernard Lyon-1, UFR Sciences de la Terre, Villeurbanne

PA: “Palaeozoic Arthropoda” collections, University Museum, University of Tokyo

SNUP: Paleontological collections, Seoul National University

UM: Université de Montpellier

VOMN: Daniel Vizcaïno collection, Carcassonne

2. Geologic setting and stratigraphy

The Taebaeksan Basin occupies the mid-eastern part of the Korean peninsula and comprises mainly the Cambro-Ordovician Choson Supergroup and Perm-Carboniferous Pyongan Supergroup (Fig. 1). The Choson Supergroup rests unconformably on the Precambrian granitic gneiss and metasedimentary rocks, and is overlaid unconformably by post-Ordovician sedimentary rocks. The Lower Palaeozoic sediments are shallow marine deposits and consist of carbonate, sandstone, and shale. In the Early Palaeozoic, the Taebaeksan Basin was a shallow marine siliciclastic-carbonate system with progressively deeper water to the west (Yongwol area; Chough et al., 2000). This siliciclastic-carbonate system persisted throughout the Cambrian. During the Ordovician, rapid accumulation of carbonate sediments in Yongwol

area resulted in the formation of a widespread carbonate platform across the Taebaeksan Basin. Sedimentological features reveal that this carbonate platform was characterized by low-relief topography with scattered shoals, lagoons, and tidal flats (Choi et al., 2001). The marine sedimentation ceased over the whole Taebaeksan Basin in the Late Ordovician, and most of the Taebaeksan Basin was emergent during the mid-Palaeozoic until marine transgression resumed in the Late Carboniferous.

The Choson Supergroup is a siliciclastic-carbonate succession ranging from the late Early Cambrian to the early Late Ordovician. Kobayashi et al. (1942) first recognized that the lithologic successions of the Choson Supergroup were different from place to place and consequently designated five types of sequences in the Choson Supergroup: namely, Tuwibong-type, Yongwol-type, Chongson-type, Pyongchang-type, and Mungyong-type sequences. These stratigraphic terms were widely used in Korea, until Choi (1998a) noted the inappropriate stratigraphic nomenclature of the Choson Supergroup and proposed the Taebaek, Yongwol, Yongtan, Pyongchang, and Mungyong groups to replace the Tuwibong-type, Yongwol-type, Chongson-type, Pyongchang-type, and Mungyong-type sequences, respectively.

The Taebaek Group is distributed in the eastern half of the Taebaeksan Basin (Fig. 1) and comprises the Changsan/Myonsan, Myobong, Taegi, Sesong, Hwajol, Tongjom, Tumugol, Makkol, Chigunsan, and Tuwibong formations in ascending order (Kobayashi, 1966; Choi, 1998a). The conventional Cambrian–Ordovician boundary was placed at the base of the Tongjom Formation (Kobayashi, 1966). The Tongjom Formation is composed mainly of light to dark gray sandstone with lesser amounts of shale and limestone. The Tumugol Formation is primarily an alternating sequence of limestones and shales with occasional limestone conglomerate beds. It yields diverse and relatively abundant fossils including trilobites, brachiopods, bivalves, gastropods, cephalopods, echinoderms, and conodonts (Kobayashi, 1934; Choi and Lee, 1988; Seo et al., 1994). The trilobite faunal assemblages, represented by *Asaphellus*, *Protopliomerops* and *Kayseraspis* Zones (Kobayashi, 1934; Kim et al., 1991), are closely comparable to the upper Tremadocian to lower Arenigian faunas of North China (Zhou and Fortey, 1986).

3. Fossil localities, associated fauna and age

All studied specimens were collected from two separate localities of the Tumugol Formation: the Tongjom section, approximately 15 km southeast of Taebaek, and the Sokkaejae section, about 9 km farther east (Figs. 1,2).

The Tongjom section is located on the western flank of a river bed where two streams merge to form a relatively wide channel at the uppermost reach of the Naktong River. It measures ca. 120 m in thickness, including a 57-m-thick

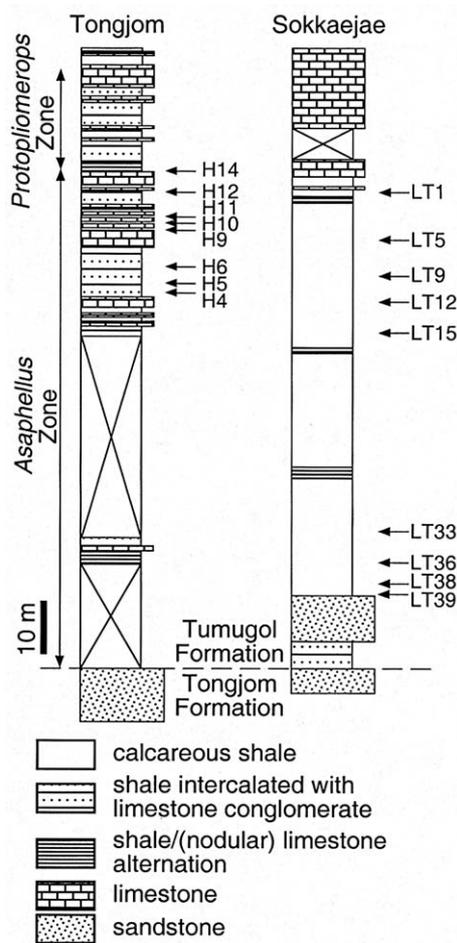


Fig. 2. Generalized columnar sections of the two localities of the Tumugol Formation at the Tongjom and Sokkaejae sections, showing lithology and fossil horizons.

Logs stratigraphiques de la Formation de Tumugol, réalisés le long des coupes de Tongjom et Sokkaejae, avec indication de la lithologie et des niveaux fossilifères ayant fourni des adorales de kirkocystidés.

concealed portion at the base and represents approximately the lower two-thirds of the Tumugol Formation (Fig. 2). The Tumugol Formation at the section comprises shale, calcareous shale, nodular limestone, lime mudstone, grainstone to packstone, and limestone conglomerate. The sediments are thought to have been deposited on a shallow ramp, strongly influenced by storm activities. The limestone conglomerates were interpreted as a product of storm activities (Lee and Kim, 1992). On the other hand, Kwon et al. (2002) reinterpreted most (more than 90%) of the limestone conglomerate as diagenetic conglomerates formed by autoconglomeration (Chough et al., 2000). Kim et al. (1991) recognized three trilobite biozones within the Tumugol Formation: namely, the *Asaphellus*, *Protopliomerops*, and *Kayseraspis* zones in ascending order. The *Asaphellus* and *Protopliomerops* zones are assigned to the upper Tremadocian, whilst the *Kayseraspis* Zone to the lower Arenigian. Skeletal elements of kirkocystid mitrates were collected from the *Asaphellus* Zone of the section, which yields trilobites (*Asaphellus coreanicus*, *A. tomkolensis*, *Hystricururus* sp.), brachiopods (*Lingulella*

sp., *Eoorthis* sp.), echinoderms (isolated plates of stylophorans, pelmatozoan stems), *Sphenothallus*, and *Plumulites* (Choi and Lee, 1988; Choi and Kim, 1989; Choi, 1990).

The Sokkaejae section lies along a mountain trail at the elevation of approximately 1000 m. It includes a nearly complete succession of the Taebaek Group (about 1400 m thick). The thickness of the Tumugol Formation is about 210 m (Fig. 2). The lower part (20 m) comprises nodular limestone, dark gray coarse-grained sandstone, and limestone conglomerate. The middle part (78 m) is characterized by a monotonous lithology composed largely of calcareous shale. The upper part (113 m) is an alternating succession of ribbon rock, bioturbated limestone, limestone conglomerate, and bioclastic grainstone to packstone. The shale facies yields relatively abundant invertebrate fossils including trilobites, brachiopods, gastropods, ostracods, plumulitids, and stylophoran echinoderms. Other parts of the formation are poor in fossils. Kirkocystid mitrates occur commonly in the middle calcareous shale. *Dikelokephalina* and *Apatokephalus* are the dominant trilobites of the lower part of the shale facies, whilst *Kayseraspis* and *Asaphopsoides* are confined to the upper part. *Apatokephalus* is a cosmopolitan late Tremadocian trilobite, and *Dikelokephalina* is restricted to the upper Tremadocian of Korea, China, and Australia (Choi et al., 2001). *Kayseraspis* and *Asaphopsoides* range through the upper Tremadocian and Arenigian sediments globally (Choi, 1998b).

The Tongjom and Sokkaejae sections have yielded about 150 isolated skeletal elements of stylophoran echinoderms (cornutes and kirkocystid mitrates), all preserved as empty moulds in approximately 40 slabs of calcareous shales. Most fragments (about 75%) are attributed to kirkocystid mitrates, and comprise isolated adorals (about 48%), marginals (about 12%), and arm elements, such as stylocones, ossicles or cover plates (about 15%). Isolated cornute fragments are less numerous (about 25%) and consist mainly of marginal elements (about 18%) and brachials (about 7%). Disarticulated skeletal elements of cornutes and kirkocystids are associated with numerous fragments of the machaeridian *Plumulites* (Kobayashi, 1960; Choi and Lee, 1988; Choi and Kim, 1989), as in some levels from the Saint-Chinian Formation (Lower Arenigian) of Montagne Noire, France (Vizcaïno et al., 2001). All stylophoran specimens from the Tremadocian of Korea are disarticulated. Such a poor preservation is common for stylophorans, which are weakly articulated forms belonging to the lowest taphonomic grade (type 1 echinoderms) defined by Brett et al. (1997). However, the preservation of very delicate portions of the organisms, such as non-disrupted portions of the arm as well as the absence of signs of wear, are both suggestive of in situ disarticulation.

4. Morphology of kirkocystid adorals

Kirkocystidae are the most abundant and diverse peltocystid mitrates. Their stratigraphic range extends from late

Tremadocian to Ashgillian. Their geographic distribution is world-wide, and includes Bohemia (Barrande, 1872, 1887; Chauvel, 1941; Ubaghs, 1979; Jefferies, 1986; Lefebvre, 1999; Parsley et al., 2000), Scotland (Jones and Woodward, 1895; Reed, 1907; Jefferies and Daley, 1996; Lefebvre, 1999), Montagne Noire (Thoral, 1935; Dean, 1966; Vizcaïno and Lefebvre, 1999), Brittany (Chauvel, 1941, 1981; Lefebvre, 1999, 2000a), Oklahoma (Bassler, 1950; Parsley, 1982, 1991), Korea (Kobayashi, 1960; Choi and Lee, 1988, Choi and Kim, 1989), Morocco (Chauvel, 1966, 1971; Cripps, 1990; Beisswenger, 1994; Lefebvre, 1999), Pennsylvania (Derstler, 1979), Wales (Jefferies, 1987; Lefebvre, 1999), Spain (Domínguez and Gutiérrez, 1990; Gutiérrez-Marco et al., 1999), Tennessee (Parsley, 1991), England (Vizcaïno and Lefebvre, 1999; Lefebvre, 1999, 2000b), Nevada and Utah (Parsley et al., 2000), and possibly Sweden (Hadding, 1913; but see Domínguez and Gutiérrez, 1990). Kirkocystids include the two genera *Anatifopsis* and *Balanocystites*. *Anatiferocystis*, *Kirkocystis*, and *Guichenocarpus* are here considered as junior synonyms of *Anatifopsis*, and *Sagittacystis* as a junior synonym of *Balanocystites* (Jefferies, 1986; Domínguez and Gutiérrez, 1990; Lefebvre, 1999, 2001, 2003).

4.1. Orientation and general organization of kirkocystids

Kirkocystids share the same basic organization as all other stylophorans, with a single, long, tripartite, flexible appendage (aulacophore) articulated to a massive, flattened, calcite-plated body (theca; Fig. 3(1)). The aulacophore has been variously interpreted as equivalent to a stem (Chauvel, 1941; Philip, 1979; Kolata et al., 1991), a feeding arm (Ubaghs, 1961, 1981; Nichols, 1972, Chauvel, 1981; Parsley, 1988), and a chordate-like tail (Jefferies, 1967, 1986; Jefferies and Daley, 1996; Domínguez et al., 2002). The stylophoran appendage is here considered as a feeding-structure, with its median and distal portions equivalent in morphology to a single crinoid or ophiuroid arm (Lefebvre, 1999; David et al., 2000). In this interpretation, the mouth was located at the base of the arm, in a deep notch borne by the first brachial (stylocone). From the location of the mouth results the orientation of the fossil, with the arm, anterior, and the theca, posterior (Fig. 3(1)). As in other stylophorans, the kirkocystid theca is flattened, with two contrasted surfaces: a flat to slightly concave lower surface, and a strongly convex upper surface (Fig. 3(2, 4)). Descriptive terms such as “adaxial” and “abaxial” will be used below so as to refer to the location of structures, respectively, towards or away from the axis of symmetry of stylophorans, which runs along the aulacophore and perpendicularly to the anterior edge of the theca (Ubaghs, 1967, 1969; Fig. 3(3)).

In all stylophorans, two or three plates surround the aulacophore insertion on the anterior edge of the upper thecal surface: the adorals (Ubaghs, 1967; Lefebvre, 1999, 2001). In kirkocystid mitrates, two adorals are present: A_1 (on the right) and A'_1 (on the left). Their morphology clearly differs

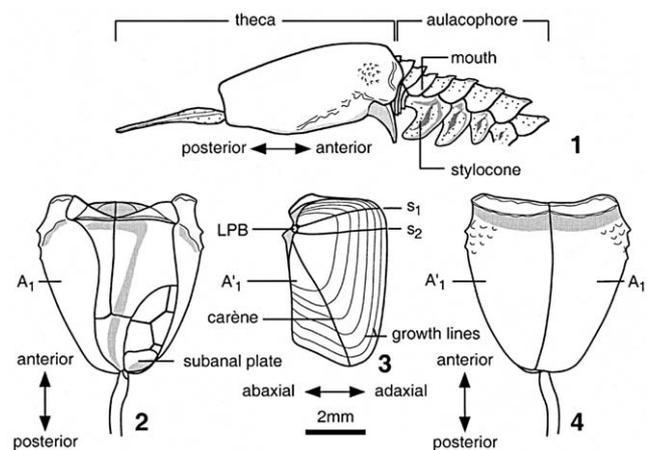


Fig. 3. Morphology of the kirkocystid mitrate *Anatifopsis trapeziiformis* Thoral, 1935. Saint-Chinian Formation, Lower Arenigian of Montagne Noire, France. 1. Right lateral view; redrawn after Lefebvre (1999: Fig. 77.7). 2. External aspect of lower thecal surface; new reconstruction mostly elaborated from specimens VOMN 116, VOMN 2793, VOMN 3026, and VOMN 3540. 3. Internal mould of the left adoral; new reconstruction mostly based on specimens FSL 168706-8, UM 45 (lectotype), and VOMN 427. 4. External aspect of upper thecal surface; new reconstruction mostly elaborated from specimens FSL 170887, VOMN 116, VOMN 857, VOMN 2793, and VOMN 3372. Abbreviations: LPB, left pyriform body.

Morphologie du mitrate kirkocystid *Anatifopsis trapeziiformis* Thoral, 1935. Formation de Saint-Chinian, Arénigien inférieur de la Montagne Noire, France. 1. Vue latérale droite; redessiné d'après Lefebvre (1999: Fig. 77.7). 2. Aspect externe de la face inférieure de la thèque; nouvelle reconstruction élaborée principalement à partir des spécimens VOMN 116, VOMN 2793, VOMN 3026, et VOMN 3540. 3. Moule interne de l'adorale gauche; nouvelle reconstruction s'appuyant en grande partie sur les échantillons FSL 168706-8, UM 45 (lectotype) et VOMN 427. 4. Aspect externe de la face supérieure de la thèque; nouvelle reconstruction principalement élaborée à partir des spécimens FSL 170887, VOMN 116, VOMN 857, VOMN 2793, et VOMN 3372. Abréviations: LPB, mamelon gauche.

from that of similar plates in other stylophorans. In kirkocystids, A_1 and A'_1 are very large, subequal, rectangular to trapezoidal skeletal elements covering the whole upper thecal surface as well as the abaxial edges of the lower surface (Fig. 3(2, 4)). Extension of adorals onto the lower surface is typically greater in *Anatifopsis* than in *Balanocystites*. The two genera show distinct adoral morphologies, correlated with different locations of the subanal plate (Lefebvre, 1999). In *Balanocystites*, the adorals are long and narrow, nearly symmetrical, with a sharp posterior adaxial extremity, as the subanal plate is located on the lower surface. In *Anatifopsis*, adorals are shorter, broad, asymmetrical, with a truncated posterior end, as the subanal plate occurs in a sub-vertical position, at the posterior end of the theca (Fig. 3(2)). The asymmetry of adorals in *Anatifopsis*, with A_1 frequently longer and narrower than A'_1 , results from the oblique course of the subanal plate (Chauvel, 1981).

4.2. Anatomy of internal moulds of kirkocystid adorals

Internal moulds of isolated kirkocystid adorals have been already described several times (Barrande, 1872; Reed, 1907; Thoral, 1935; Chauvel, 1941, 1966; Kobayashi, 1960;

Choi and Kim, 1989; Domínguez and Gutiérrez, 1990; Jefferies and Daley, 1996; Lefebvre, 1999). The internal morphology of kirkocystid adorals remains poorly understood, because of their interpretation, in most cases, as disarticulated crustacean valves. The presence of one, and in most cases, two deep anterior transverse grooves in internal moulds of kirkocystid adorals has been pointed out by most of the authors (Barrande, 1872; Chauvel, 1941, 1966; Kobayashi, 1960; Domínguez and Gutiérrez, 1990; Lefebvre, 1999). These two grooves (“sillons”) were designated “s₁” (anteriorly) and “s₂” (posteriorly) by Chauvel (1941, 1966). They correspond to two strong, internal, transverse ridges (septa) running from the adaxial (upper) border of the adoral and converging towards the opposite, abaxial (lower) edge of the plate (Fig. 3(3)). The two ridges corresponding to s₁ and s₂ are designated here “Anterior Internal Crest” (AIC), and “Posterior Internal Crest” (PIC), respectively. Internal moulds of kirkocystids are thus divided into three regions (anterior, median, and posterior) by s₁ and s₂. In *Anatifopsis*, s₁ and s₂ are nearly parallel to each other, and converge forming a small angle (about 10°). In *Balanocystites*, the angle between s₁ and s₂ is greater (about 20°).

Important new data on the morphology of internal moulds of kirkocystid adorals have been evidenced from the careful examination of the new Korean material, and its comparison with adorals belonging to other kirkocystids and mitrates. A key observation is the fundamentally different nature of the AIC and PIC. The AIC corresponds to a sharp transverse ridge on the internal surface of adorals (Fig. 4(4, 6, 8, 9)). It forms the boundary between the aulacophore insertion cavity (anteriorly) and the co-operculum (posteriorly). As defined by Ubahgs (1967), the co-operculum is a concave, cupular, symmetrical platform developed on the lower (internal) surface of each adoral in mitrates. Each co-operculum was articulated in life to a similar cupular structure (scutula) carried by the upper edge of the underlying skeletal element (Ubahgs, 1967; Lefebvre, 2001). Co-opercula (above) and scutulae (below) define together two cavities (right and left) that were nearly totally occluded in life. In internal moulds, these cavities correspond to two crescentic, pear-shaped bodies designated either “mamelons” (Chauvel, 1941; Ubahgs, 1967) or “pyriform bodies” (Fig. 3(3); Jefferies, 1986; Lefebvre, 2001).

The PIC forms the posterior wall of the co-operculum and corresponds to the sharp anterior edge of a narrow transverse strip of calcite flooring the internal surface of adorals. In internal moulds, this narrow strip of calcite corresponds to a narrow, slightly depressed transverse zone located posteriorly to s₂ (Fig. 4(1–3, 5, 7)). The most anterior groove, s₁, is present in all specimens, whereas s₂ is sometimes absent, when the internal layer is broken off (preservational bias; see Fig. 4(9)). Comparison with *Peltocystis* and *Mitrocystella* suggests that the narrow PIC-strip of calcite in kirkocystid adorals is equivalent to the much more extensive internal calcitic layer flooring adorals in other mitrates. Dissection of several internal moulds of adorals belonging to the Bohe-

mian kirkocystid *Balanocystites primus* shows the presence of another, more posterior strip of calcite that plunges from the posterior wall of the co-operculum towards the center of the intrathecal cavity (Lefebvre, 1999). This internal process is connected to the PIC-strip of calcite and thus possibly represents a posterior, upturned, finger-like portion of the internal layer. Each process from the internal calcitic layer of kirkocystid adorals (PIC-strip and internal strip) bears a deep transverse groove (Fig. 4(6, 8)). In kirkocystids, these grooves converge towards a depressed area posterior to co-opercula, and form a ramified structure. This radiating structure is similar in morphology and location to the “palmar complex” described in mitrocystitids (Chauvel, 1941; Jefferies, 1967). A similar pattern of radiating groove-bearing structures borne by the internal calcitic layer of adorals has been shown also in jaekelocarpid peltocystids (Kolata et al., 1991; Domínguez et al., 2002). Consequently, comparison with mitrocystitid mitrates suggests that radiating grooves borne by the internal calcitic layer of adorals in kirkocystid and jaekelocarpid mitrates possibly represent the imprint of the palmar complex. This is a very important observation and the first report of the possible occurrence of the palmar complex in peltocystid mitrates.

The presence of numerous, concentric growth lines on the internal surface of the external calcitic layer of adorals has been mentioned by several authors (Barrande, 1872; Thoral, 1935; Chauvel, 1941, 1966, 1981; Kobayashi, 1960; Choi and Kim, 1989; Domínguez and Gutiérrez, 1990; Jefferies and Daley, 1996; Lefebvre, 1999). The concentric arrangement of growth lines suggests that the growth center of adorals is the region of the co-operculum. Growth lines are parallel to the anterior, adaxial (upper), and posterior edges of the plate, but oblique to the abaxial (lower) border (Figs. 3(3) and 4(1–3, 5, 13)). Anteriorly, the transition from transverse growth striae (parallel to the anterior thecal border) to longitudinal growth lines (parallel to the adaxial edge) occurs along s₁. Posteriorly, the transition from longitudinal striae to transverse growth lines (parallel to the posterior edge of the theca) occurs along an oblique, slightly depressed line: the “carène” (Thoral, 1935; Chauvel, 1966; Domínguez and Gutiérrez, 1990; Lefebvre, 1999). The carène runs from the anterior abaxial extremity of the adoral (close to the pyriform body) towards the opposite, posterior end of the plate (Fig. 3(3)). As growth lines are located on the internal surface of the adoral, they are not visible below the PIC-strip of calcite (Fig. 4(1, 2, 6)).

4.3. Characterization of adoral shape

Definition of a standard of orientation for kirkocystid adorals: Precise measurements are particularly difficult to obtain on strongly convex objects, such as internal moulds of kirkocystid adorals. So as to minimize problems of parallax, a standardized orientation is needed for kirkocystid adorals (Fig. 5(4)). All internal moulds were drawn using camera-lucida method, at the same scale, and perpendicularly to a

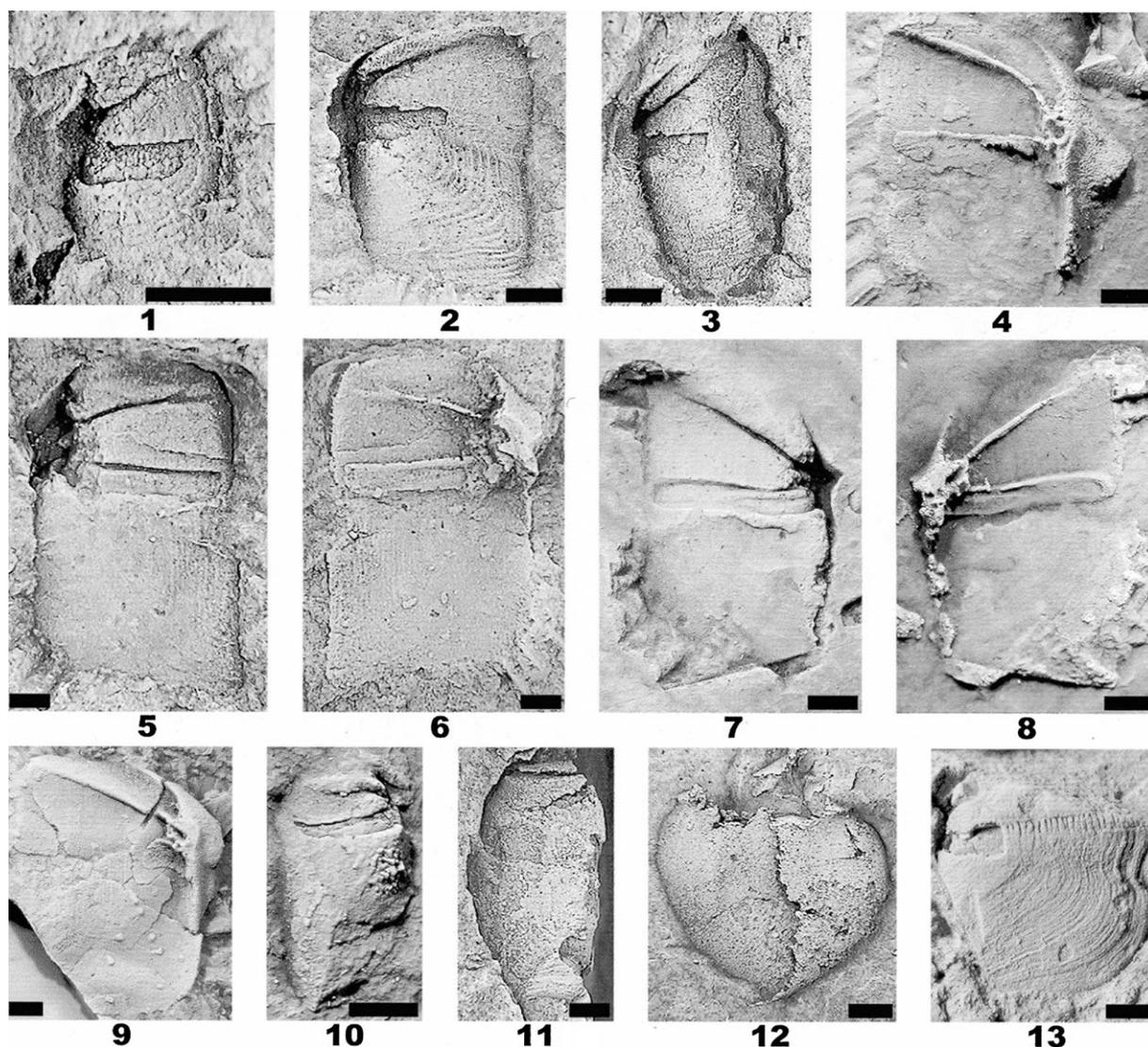


Fig. 4. Kirkocystid adorals; all scale bars are 1 mm in length. **1–9.** Morphotype A adorals, Tumugol Formation (*Asaphellus* Zone, Tremadocian), Korea. **1.** SNUP 2521: natural internal mould of a left adoral, Sokkaejae (LT36). **2.** SNUP 2526: natural internal mould of a left adoral, Sokkaejae (LT15). **3.** SNUP 136: natural internal mould of a left adoral, Tongjom (H14). **4.** SNUP 20: latex cast of a left adoral, Tongjom (H11). **5, 6** SNUP 2525: left adoral, Sokkaejae (LT33); internal mould (**5**) and latex cast (**6**). **7, 8** SNUP 54: right adoral, Tongjom (H6); internal mould (**7**) and latex cast (**8**). **9** SNUP 2546: latex cast of a left adoral, Sokkaejae (LT9). **10.** SNUP 2545: *Anatifopsis* sp. (morphotype B), Tumugol Formation (*Asaphellus* Zone, Tremadocian), Sokkaejae (Korea); natural internal mould of a right adoral. **11.** UM 210: *Anatifopsis trapeziiformis*, syntype, figured in Thoral (1935: Pl. 11, Fig. 5), Saint-Chinian Formation (Lower Arenigian), Montagne Noire (France); natural mould of right adoral. **12.** CGSP JH1100: specimen of a juvenile kirkocystid, Sárka Formation (Aberedidion), Bohemia; latex cast of upper thecal surface (external aspect). **13.** PA 2422: *Anatifopsis truncata*, holotype, figured in Kobayashi (1960: Pl. 13, Fig. 1), Mungok Formation (Tremadocian), Yongwol (Korea); natural mould of left adoral.

Adorales de kirkocystidés ; toutes les barres d'échelle représentent 1 mm. **1–9.** Adorales du morphotype A, Formation de Tumugol (Zone à *Asaphellus*, Trémadocien), Corée. **1.** SNUP 2521: moule interne d'une adorale gauche, Sokkaejae (niveau LT36). **2.** SNUP 2526: moule interne d'une adorale gauche, Sokkaejae (niveau LT15). **3.** SNUP 136: moule interne d'une adorale gauche, Tongjom (niveau H14). **4.** SNUP 20: moulage en latex d'une adorale gauche, Tongjom (niveau H11). **5, 6.** SNUP 2525: adorale gauche, Sokkaejae (niveau LT33) ; moule interne (**5**) et moulage en latex (**6**). **7, 8** SNUP 54: adorale droite, Tongjom (niveau H6) ; moule interne (**7**) et moulage en latex (**8**). **9.** SNUP 2546: moulage en latex d'une adorale droite, Sokkaejae (niveau LT9). **10.** SNUP 2545: *Anatifopsis* sp. (morphotype B), Formation de Tumugol (Zone à *Asaphellus*, Trémadocien), Sokkaejae (Corée) ; moule interne d'une adorale droite. **11.** UM 210: *Anatifopsis trapeziiformis*, syntype figuré par Thoral (1935: Pl. 11, Fig. 5), Formation de Saint-Chinian (Arenig inférieur), Montagne Noire (France) ; moule interne de l'adorale droite. **12.** CGSP JH1100: spécimen de kirkocystidé juvénile, Formation de Sárka (Aberedidion), Bohême ; moulage en latex de la face supérieure de la thèque (aspect externe). **13.** PA 2422: *Anatifopsis truncata*, holotype figuré par Kobayashi (1960: Pl. 13, Fig. 1), Formation de Mungok (Trémadocien), Yongwol (Corée) ; moule interne de l'adorale gauche.

virtual plane surface defined by two lines: the adaxial (upper) edge of the adoral and the line of maximal curvature of the abaxial (lower), opposite side.

Measurements: Measurements have been made directly on camera-lucida drawings. All adorals have been drawn in

the same orientation, with the anterior region at the top, the posterior region at the bottom, and the adaxial (upper) edge in a vertical position. Measurements have been made on external adoral outlines, and when possible, on several growth lines as well, so as to investigate possible

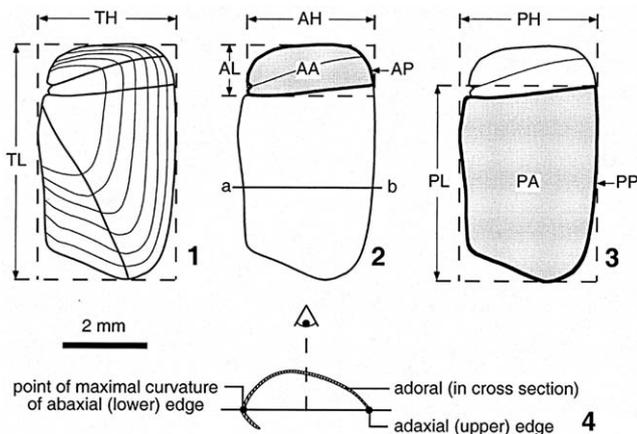


Fig. 5. Characterization of adoral shape in kirkocystid mitrates. 1. Measurements made on adoral outlines. 2. Measurements made on the anterior portion of adorals. 3. Measurements made on the posterior region of adorals. 4. Cross-section of a–b indicated in 2; standardized orientation adopted for camera-lucida drawings of kirkocystid adorals. Abbreviations: AA, anterior area; AH, anterior height; AL, anterior length; AP, anterior perimeter; PA, posterior area; PH, posterior height; PL, posterior length; PP, posterior perimeter; TH, thecal height; TL, thecal length.

Caractérisation de la forme des adorales de mitrates kirkocystidés. 1. Mesures réalisées sur les contours de l'adorale. 2. Mesures portant sur la partie antérieure de l'adorale. 3. Mesures décrivant la partie postérieure de l'adorale. 4. Section transversale de l'adorale suivant le trait de coupe a–b indiqué en 2; orientation standard adoptée pour dessiner les adorales de kirkocystidés à la chambre claire. Abréviations : AA, aire de la région antérieure ; AH, hauteur de la région antérieure ; AL, longueur de la région antérieure ; AP, périmètre de la région antérieure ; PA, aire de la région postérieure ; PH, hauteur de la région postérieure ; PL, longueur de la région postérieure ; PP, périmètre de la région postérieure ; TH, hauteur totale ; TL, longueur totale.

morphological changes during ontogeny. In this study, 10 parameters were measured from three different surfaces, corresponding to (1) the general outline of the adoral (or growth line), (2) its anterior portion (anteriorly to s_2), and (3) its posterior region (posteriorly to s_2). The morphology of each general outline has been described by two parameters, corresponding to the total height TH, and the total length TL (Fig. 5(1)). Four parameters (length L, height H, perimeter P, and area A) have been extracted both from the anterior portion (AL, AH, AP, and AA, respectively) and the posterior region (PL, PH, PP, and PA, respectively) of each general outline (Fig. 5(2, 3)).

Variables used in the study: A dorals of Korean kirkocystids are 2–8 times smaller than those of most European or North African forms. This observation makes it necessary to work on non-dimensional variables so as to concentrate on the morphology of adorals and to minimize size effect. Eight non-dimensional variables have been used in this study. They correspond to ratios calculated using the 10 above mentioned uni- or bidimensional parameters: coefficient of elongation CE ($CE = TL/TH$), surface ratio SR ($SR = PA/AA$), relative anterior height RAH ($RAH = AH/TL$), relative anterior length RAL ($RAL = AL/TL$), relative anterior perimeter RAP ($RAP = AP/TL$), relative posterior height RPH ($RPH = PH/TL$), relative posterior length

RPL ($RPL = PL/TL$), and relative posterior perimeter RPP ($RPP = PP/TL$).

5. Morphometric analyses of kirkocystid adorals

Observation of more than 60 internal moulds of kirkocystid adorals from the Tumugol Formation shows that these isolated skeletal elements display a particularly wide array of possible morphologies. For example, s_1 and s_2 can be more or less parallel (Fig. 4(5)) or strongly diverging adaxially (Fig. 4(7)). Morphology of the adaxial (upper) edge of adorals is also very variable and ranges from strongly convex, with a rounded posterior end (Fig. 4(1, 4, 7, 8)), to straight, with a sharp, angular posterior extremity (Fig. 4(2, 5, 6)). Such a great variability questions the possible presence of several morphotypes in the new Korean material that could be related to the co-occurrence of different species or to a possible asymmetry between left and right adorals (as in some other kirkocystids). Another interesting aspect of isolated adorals of Korean kirkocystids is their extremely short and broad morphology, characterized by the reduced extension of their posterior region (posteriorly to s_2) relative to that of the two more anterior regions. The morphology of Korean adorals clearly differs from that of most other kirkocystids, but it strongly recalls that of adorals in juvenile specimens belonging to other kirkocystid species (Fig. 4(12); see also Parsley et al., 2000: Pl. 2, Figs. 6 and 7).

5.1. Adorals of Korean Kirkocystidae

The aims of this analysis focusing on Korean adorals are (1) to compare the morphology of the new specimens (Tumugol Formation) with that of the type material of *Anatifop-*

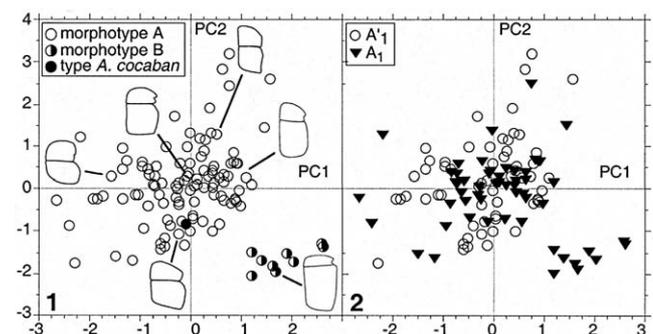


Fig. 6. Plots of morphospace occupation of 114 growth stages corresponding to 32 adorals of Korean kirkocystids from the Tumugol and Mungok formations (*Asaphellus* Zone, Tremadocian) on the first two principal components. 1. Distinction between morphotypes A and B, and location of the lectotype of *Anatifopsis cocaban* (PA2419). 2. Distinction between left (A_1) and right (A_1) adorals.

Projections dans le plan factoriel PC1-PC2 de l'espace morphologique de 114 stades de croissance correspondant à 32 adorales de kirkocystidés coréens des formations de Tumugol et Mungok (Zone à *Asaphellus*, Trémadocien). 1. Distinction des morphotypes A et B, avec position du lectotype d'*Anatifopsis cocaban* (PA2419). 2. Distinction entre adorales gauches (A_1) et droites (A_1).

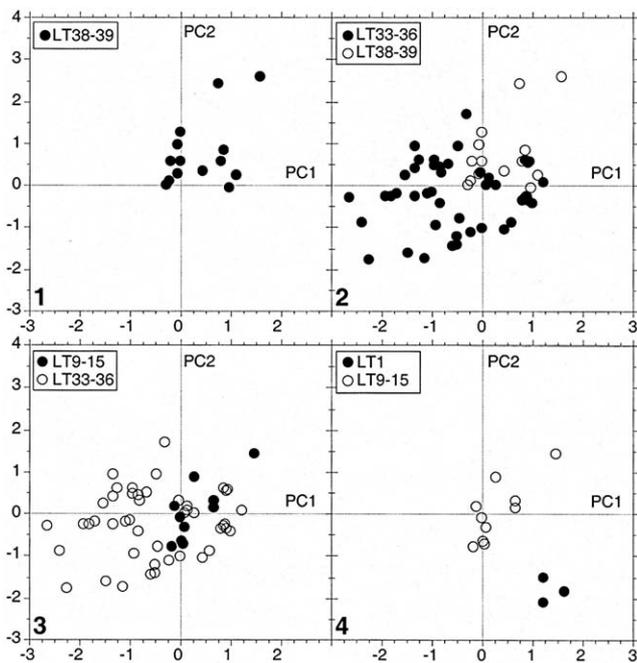


Fig. 7. Evolution of morphospace occupation of 73 growth stages corresponding to 20 adorals of Korean kirkocystids from the Sokkaejae section (Tumugol Formation, *Asaphellus* Zone, Tremadocian), on the first two principal components. Empty circles correspond to morphospace occupation in the previous stage. 1. Morphospace occupation in stratigraphic levels LT38–39. 2. Stratigraphic levels LT38–39 and LT33–36. 3. Stratigraphic levels LT33–36 and LT9–15. 4. Stratigraphic levels LT9–15 and LT1.

Projections dans le plan factoriel PC1–PC2 illustrant l'évolution, au cours du temps, de l'espace morphologique occupé par 73 stades ontogénétiques correspondant à 20 adorales de kirkocystidés coréens de la coupe de Sokkaejae (Formation de Tumugol, Zone à *Asaphellus*, Trémadocien). Les cercles vides représentent la position des points du niveau stratigraphique antérieur. 1. Niveaux stratigraphiques LT38–39. 2. Niveaux stratigraphiques LT38–39 et LT33–36. 3. Niveaux stratigraphiques LT33–36 et LT9–15. 4. Niveaux stratigraphiques LT9–15 et LT1.

sis cocaban (Mungok Formation), and (2) to investigate their great morphological variability, so as to determine if it corresponds to a large, continuous spectrum of morphology or to the juxtaposition of several morphotypes that could be correlated, for example, to the co-occurrence of different species or to problems of asymmetry between left and right adorals.

Material and methods: About half of the new material of Korean adorals was too poorly preserved to make precise measurements and had to be excluded from the morphometric analysis (broken or incomplete specimens). Consequently, only 31 adorals from the Tumugol Formation (on a total number of about 70) have been used for the analysis. The lectotype of *A. cocaban* (Kobayashi, 1960: Pl. 13, Fig. 3; Choi and Kim, 1989: p. 409) from the Mungok Formation (Tremadocian) has been also included in this study, so as to compare its morphology with the wide morphological spectrum exhibited by kirkocystids from the Tumugol Formation. The holotype of *Anatifopsis truncata* (Kobayashi, 1960: Pl. 13, Fig. 1), also from the Mungok Formation, could not be considered here, as its anterior region is too poorly preserved (Fig. 4(13)). However, re-examination of the type material of Kobayashi (1960) indicates that adorals of *A. cocaban* and

A. truncata are very similar to each other (e.g. reduced extension of posterior region), with the exception of their adaxial (upper) edges. The adaxial edge is straight to slightly concave in *A. cocaban*, whereas it shows a deep concave notch, posteriorly to s_2 in *A. truncata* (Fig. 4(13)). This notch is not a preservational feature, as it can be clearly evidenced in more internal growth lines of at least two specimens from the Mungok Formation. Such an adaxial notch has not been observed in any of the new adorals from the Tumugol Formation.

The 32 retained specimens consist of 17 left (53.1%) and 15 right elements (47.9%). The inclusion of different ontogenetic stages (growth lines) for each of the 32 adorals has allowed us to obtain a total number of 114 sets of measurements (observations), which represents an average of about 3.5 ontogenetic stages for each specimen. Among these 114 observations, 59 (51.7%) correspond to left adorals, and 55 (48.3%) to right elements.

Eight variables (CE, SR, RAH, RAL, RAP, RPH, RPL, RPP) have been calculated for 114 observations (ontogenetic stages of kirkocystid adorals). This resulted in a large data matrix (114 × 8). This matrix has been processed by Principal Component Analysis (PCA) using the software Statview (version 4.51.1). PCA provides a means of synthesizing optimally such a large quantity of information into a reduced number of major components of variation. Generally, only most significant principal components (with eigen values >1) are extracted. Principal components are interpretable factors defining a multidimensional space, in which observations can be plotted. This ordination of observations according to similarities in shape provides a graphical representation of morphological diversity. Such a picture of disparity based on measurements made on actual specimens corresponds to an empirical morphospace, as defined by McGhee (1999).

Results: PCA of eight variables calculated from 114 ontogenetic stages of adorals of Korean kirkocystids provides a significant result, with 89.4% of the variation represented on the first two principal components (Fig. 6). PC1 and PC2 define a two-dimensional morphospace, in which morphological diversity of adorals is expressed with a loss of 10.6% of the variation in the data set. PC1 (57.6% of the variance) is primarily influenced by the anterior region of adorals (RAH, RAL, and mostly RAP) but also by the coefficient of elongation (CE) and the relative height of the posterior area (RPH; see Table 1). PC2 (31.8% of the variance) is mainly related to the posterior region of adorals (RPL, and mostly RPP) and to the surface ratio (SR; Table 1). The high loadings observed for the two variables related to perimeter, both on PC1 (RAP) and on PC2 (RPP), suggest that the result of a bivariate plot of RAP against RPP would not much differ from that computed by the multivariate analysis. Morphospace occupation is irregular, and two clearly distinct sets of adorals (morphotypes) can be evidenced (Fig. 6(1)). The first one occupies a large, oblique portion of the morphospace (great morphological variability) and it includes the lectotype of *A. cocaban*. This first morphotype groups 105 ontogenetic stages

Table 1

Morphometric analysis of kirkocystid adorals from the Tumugol and Mungok formations. Character loadings on the first two principal components. Bold values indicate significant character loadings. See text for definition of variables.

Analyse morphométrique des adorales de kirkocystidés des formations de Tumugol et Mungok. Scores des différentes variables sur les deux principaux axes factoriels ; les valeurs en gras sont significatives. Voir texte pour la définition des variables.

	PC1	PC2
SR	-0.743	0.564
RAH	0.860	0.338
RAL	0.815	-0.421
RAP	0.968	-0.030
RPH	0.817	0.508
RPL	-0.640	0.668
RPP	0.094	0.973
CE	-0.792	0.533

(92.1%) corresponding to 30 specimens (93.7%), all characterized by a large, inflated anterior region, typically as long as high (Fig. 4(1–9)). These adorals exhibit an apparently continuous spectrum of morphologies ranging from forms with short posterior regions and curved postero-adaxial ends (negative values on PC1 and PC2) towards forms with longer posterior regions and sharp, angular postero-adaxial corners (positive values on PC1 and PC2). The second group occupies a much more reduced portion of the morphospace and corresponds to a clearly distinct, well-defined morphotype (positive values on PC1 and negative values on PC2). This morphotype corresponds to nine ontogenetic stages (7.9%) and two specimens (6.3%), all characterized by a narrow anterior region (much higher than long) and an elongate posterior region with an angular postero-adaxial extremity (Fig. 4(10)). The absence of transitional morphologies between the two groups and the very contrasted morphologies of their anterior regions both strongly support the identification of two different morphotypes within Korean adorals (Fig. 6(1)): the first one (morphotype A) is characterized by short adorals with an inflated anterior region and a great morphological variability (especially as far as the posterior region is concerned); the second one (morphotype B) corresponds to elongate adorals with a narrow anterior region.

Table 2

Sample sizes (specimens and ontogenetic stages) used for morphometric analysis of kirkocystid adorals from the Sokkaejae and Tongjom sections, Tumugol Formation (*Asaphellus* Zone), Tremadocian of Korea. Abbreviations: A_l, left adoral; A_r, right adoral.

Nombre d'échantillons (spécimens et stades ontogénétiques) utilisés pour l'analyse morphométrique des adorales de kirkocystidés des coupes de Sokkaejae et Tongjom, Formation de Tumugol (Zone à *Asaphellus*), Trémadocien de Corée. Abréviations : A_l, adorale gauche ; A_r, adorale droite.

	Stratigraphic intervals	Specimens			Ontogenetic stages		
		A _l	A _r	Total	A _l	A _r	Total
Sokkaejae section	LT1	0	1	1	0	3	3
	LT9-15	2	1	3	7	3	10
	LT33-36	8	5	13	26	20	46
	LT38-39	2	1	3	9	5	14
	Total	12	8	20	42	31	73
Tongjom section	H12-14	1	3	4	1	9	10
	H9-11	2	1	3	7	4	11
	H5-6	1	2	3	4	10	14
	Total	4	6	10	12	23	35

Distinction between left and right adorals (Fig. 6(2)) shows that left and right adorals show identical morphospace occupations in morphotype A. This observation suggests that these elements have similar morphologies, and were thus probably more or less symmetrical. Morphotype B is only represented by right adorals. This is a consequence of the low number of specimens (2) attributed to this morphotype. However, these right adorals are morphologically clearly distinct from those belonging to morphotype A. Consequently, the identification of two morphotypes within Korean adorals is not correlated to a potential dissymmetry between left and right elements.

5.2. Disparity of Korean adorals through time

The aim of this second morphometric analysis based on Korean adorals is to investigate their morphological variability through time. Temporal aspects of disparity can be documented, as adorals have been collected from several successive stratigraphic levels within the *Asaphellus* Zone of the Tumugol Formation (Fig. 2).

Material and methods: The 30 selected specimens from the Tumugol Formation (*Asaphellus* Zone, Tremadocian) have been collected in two different sections, Sokkaejae and Tongjom. In the Sokkaejae section (Fig. 2), eight different stratigraphic levels have yielded 20 specimens, corresponding to 73 ontogenetic stages. As sample size was too reduced for each stratigraphic level, these eight levels have been grouped into four intervals (Table 2). In the Tongjom section (Fig. 2), five different stratigraphic levels have yielded 10 specimens, corresponding to 35 ontogenetic stages. As for the Sokkaejae section, the five fossiliferous intervals of the Tongjom section have been grouped into three intervals (Table 2).

The same eight variables as for the previous analysis have been calculated for the 108 observations (ontogenetic stages) of kirkocystid adorals from the Tumugol Formation and reported into a large data matrix (108 × 8). This matrix has been processed by PCA using the software Statview (version 4.51.1).

Results: PCA of eight variables calculated from 108 ontogenetic stages of adorals of kirkocystids from Tumugol For-

Table 3

Morphometric analysis of kirkocystid adorals from the Tumugol Formation. Character loadings on the first two principal components. Bold values indicate significant character loadings. See text for definition of variables. Analyse morphométrique des adorales de kirkocystidés de la Formation de Tumugol. Scores des différentes variables sur les deux principaux axes factoriels ; les valeurs en gras sont significatives. Voir texte pour la définition des variables.

	PC1	PC2
SR	-0.743	0.565
RAH	0.861	0.337
RAL	0.816	-0.418
RAP	0.968	-0.028
RPH	0.818	0.508
RPL	-0.642	0.666
RPP	0.093	0.973
CE	-0.792	0.532

mation provides a significant result (89.5% of the variation represented on the first two principal components), mostly comparable to that of the previous analysis. Loadings of variables on each axis are also mostly similar to those of the first analysis (Table 3). It must be stressed that the reduced number of specimens collected in the two localities of Sokkaejae and Tongjom (20 and 10, respectively) clearly indicates that the temporal patterns of morphological changes presented below should be considered extremely cautiously, and that collection of new, more abundant material is necessary for deeper investigations. A preliminary analysis of morphospace occupation of Korean adorals through time suggests that, at least in the Sokkaejae section, morphotype A could correspond to two, stratigraphically and morphologically distinct, subsets of adorals (Fig. 7). The first one is observed in LT38-39 and re-occurs in LT9-15. It is characterized by relatively long adorals with a quadrangular postero-adaxial corner. The second subset, which is present only in the LT33-36 interval, corresponds to shorter elements with a curved postero-adaxial edge. Morphology of these short elements is comparable to that of the lectotype of *A. cocaban*. This observation questions the possible occurrence of distinct species within morphotype A. In the two localities of Sokkaejae and Tongjom, morphotype B is only observed in the highest portions of the sections (LT1 and H12, respectively), suggesting that this morphotype may appear later than morphotype A (Figs. 7,8).

5.3. Adorals of European and North African Kirkocystidae

The aim of this morphometric analysis is to focus on morphological diversity of adorals within European and North African Kirkocystidae. This study is based on a representative sample of 69 specimens (corresponding to 275 ontogenetic stages) ranging from the Tremadocian to the Caradocian. This sample includes the type material of several species of Kirkocystidae (*Anatifopsis bohémica*, *Anatifopsis balclatchiensis*, *A. escandei*, *A. longa*, and *Anatifopsis trapeziiformis*), but also numerous other specimens belonging to almost all known kirkocystid species. This exploration of

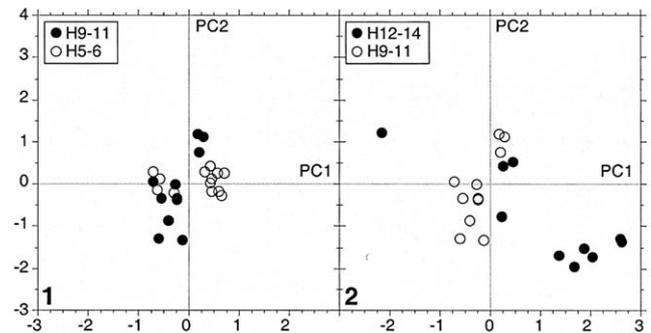


Fig. 8. Evolution of morphospace occupation of 35 growth stages corresponding to 10 adorals of Korean kirkocystids from the Tongjom section (Tumugol Formation, *Asaphellus* Zone, Tremadocian) on the first two principal components. Empty circles correspond to morphospace occupation in the previous stage. 1. Morphospace occupation in stratigraphic levels H5-6 and H9-11. 2. Stratigraphic levels H9-11 and H12-14.

Projections dans le plan factoriel PC1-PC2 illustrant l'évolution, au cours du temps, de l'espace morphologique occupé par 35 stades ontogénétiques correspondant à 10 adorales de kirkocystidés coréens de la coupe de Tongjom (Formation de Tumugol, Zone à *Asaphellus*, Trémadocien). Les cercles vides représentent la position des points du niveau stratigraphique antérieur. 1. Niveaux stratigraphiques H5-6 et H9-11. 2. Niveaux stratigraphiques H9-11 et H12-14.

the empirical morphospace of adorals within Kirkocystidae is to provide a preliminary analysis of their morphological diversity, the output of which can be used as a quantitative support for a comparison with morphotypes A and B of Korean adorals.

Material and methods: Kirkocystids have been described from Europe, North Africa, North America, and Korea (see above). North American kirkocystids have not been considered in this study for two reasons: (1) Arenigian forms from the Fillmore Formation of Utah and the Ninemile Formation of Nevada are undescribed (Sprinkle and Guensburg, 1995; Parsley et al., 2000; Sumrall pers. comm.), and (2) Caradocian specimens from the Bromide Formation of Oklahoma and the Benbolt Formation of Tennessee are only known from complete, articulated thecae (Parsley, 1982, 1991). Internal moulds of 69 adorals from almost all known occurrences of Kirkocystidae from Europe and North Africa have been included in this study, so as to provide a representative sample of their taxonomic, geographical and stratigraphical distributions. The same measurements as for Korean adorals (see above) have been made on this material, both on adoral outlines and on internal growth lines, so as to take into account possible morphological changes during ontogeny. The inclusion of different ontogenetic stages for each of the 69 selected adorals has allowed us to obtain a total number of 275 sets of measurements (observations), which represents an average of about four ontogenetic stages per specimen.

As far as *Anatifopsis* is concerned, 53 specimens (221 ontogenetic stages) have been considered (Table 4). Selected specimens of *Anatifopsis* encompass most known occurrences of that genus in Europe and North Africa. Other reported occurrences of adorals assigned to *Anatifopsis* include three poorly preserved specimens from the Upper Fez-

Table 4

Sample sizes (specimens and ontogenetic stages) used for morphometric analysis of kirkocystid adorals from Europe and North Africa (Tremadocian to Caradocian). Abbreviations: A₁, left adoral; A₁, right adoral.

Nombre d'échantillons (spécimens et stades ontogénétiques) utilisés pour l'analyse morphométrique des adorales de kirkocystidés d'Europe et d'Afrique du Nord (Trémadocien à Caradocien). Abréviations : A₁, adorale gauche ; A₁, adorale droite.

			Specimens			Ontogenetic stages		
			A ₁	A ₁	Total	A ₁	A ₁	Total
<i>Anatifopsis</i>								
Shinerton Shales	Tremadocian	Shropshire	3	4	7	11	15	26
Saint-Chinian F.	L. Arenigian	Mgne Noire	7	10	17	34	44	78
La Maurerie F.	L. Arenigian	Mgne Noire	4	4	8	15	19	34
Sarka F.	Aberdeiddian	Bohemia	1	0	1	1	0	1
Traveusot F.	Llandeilian	Brittany	1	2	3	3	8	11
Ouine-Inirne F.	Llandeilian	Morocco	3	4	7	15	18	33
Vinice F.	Caradocian	Bohemia	2	0	2	8	0	8
Zahorany F.	Caradocian	Bohemia	0	1	1	0	3	3
Balclatchie Group	Caradocian	Scotland	5	1	6	18	5	23
<i>Croz. dujardini</i> biozone	Caradocian	Spain	0	1	1	0	4	4
Total			26	27	53	105	116	221
<i>Balanocystites</i>								
Sarka F.	Aberdeiddian	Bohemia	5	2	7	20	8	28
Traveusot F.	Llandeilian	Brittany	2	3	5	2	9	11
Balclatchie Gr.	Caradocian	Scotland	3	1	4	12	3	15
Total			10	6	16	34	20	54

ouata Formation (Arenigian) of Anti-Atlas, Morocco (Chauvel, 1966), several flattened specimens preserved in shales from the Landeyran Formation (Arenigian), Montagne Noire, France (Dean, 1966; Vizcaïno and Lefebvre, 1999; Lefebvre, 1999; Vizcaïno et al., 2001), two specimens from the Postolonnec (Llandeilian) and Kermeur (Caradocian) formations of Brittany, France (Kerforne, 1901, Chauvel, 1941), several specimens from the “pizarras del Ordovicio medio” (Llandeilian) of Spain (Domínguez and Gutiérrez, 1990; Aramburu et al., 1996; Gutiérrez-Marco et al., 1999), a single posteriorly broken specimen from the Letna Formation (Caradocian) of Bohemia (*A. acuta*; Barrande, 1872), and several poorly preserved specimens from the Starfish Bed (Ashgillian) of Ayrshire, Scotland (Lefebvre, 1999). Internal moulds of *Anatifopsis* from the Upper Ordovician of Sweden have been re-identified as isolated skeletal elements of polyplacophorans (Rolfé, 1969; Domínguez and Gutiérrez, 1990).

As far as *Balanocystites* is concerned, 16 specimens (54 ontogenetic stages) have been measured (Table 4). This material comprises specimens from almost all known occurrences of *Balanocystites* in Europe and North Africa. Other mentioned occurrences of internal moulds of adorals belonging to this genus include several specimens from the La Maurerie and Landeyran formations (Arenigian) of Montagne Noire, France (Lefebvre, 1999; Vizcaïno et al., 2001) and several poorly preserved specimens from the Starfish Bed (Ashgillian) of Ayrshire, Scotland (Lefebvre, 1999).

The same eight variables as for Korean adorals have been calculated for each of the 275 observations (ontogenetic stages of adorals belonging to European and North African Kirkocystidae), and reported into a large data matrix (275 × 8), which has been processed by PCA using Statview (version 4.51.1).

Results: PCA of adorals of Kirkocystidae provides a significant result, which groups 89.7% of the variation on the first two components (Fig. 9). PC1 and PC2 define a two-dimensional morphospace, in which disparity of adorals is expressed with a loss of 10.3% of the variation in the data set. PC1 (63.3% of the variance) is mostly related to the anterior region of adorals (RAH, and mainly RAP), but also to the coefficient of elongation (CE) and the posterior region of adorals (RPH; Table 5). PC1 clearly discriminates short and broad, quadrangular adorals with a truncated posterior end on the left (e.g. *A. trapeziiformis*, *A. balclatchiensis*) from narrower, more elongate, sub-triangular ones with a sharp posterior extremity on the right (e.g. *B. primus*). PC2 (26.4%

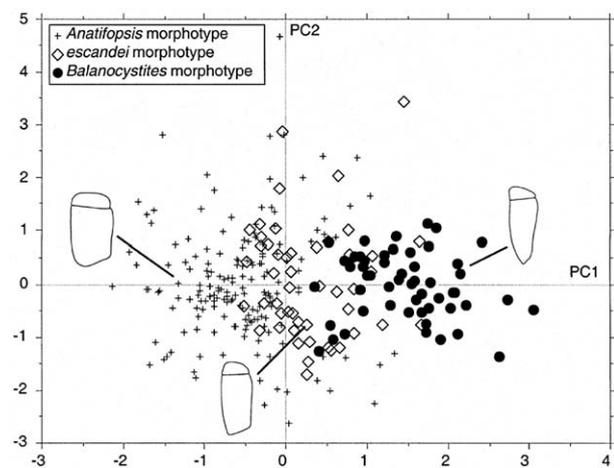


Fig. 9. Plot of morphospace occupation of 275 growth stages corresponding to 69 adorals of European and North African kirkocystids (Tremadocian to Caradocian) on the first two principal components.

Projection dans le plan factoriel PC1-PC2 de l'espace morphologique de 275 stades de croissance correspondant à 69 adorales de kirkocystidés d'Europe et d'Afrique du Nord (Trémadocien–Caradocien).

Table 5

Morphometric analysis of kirkocystid adoralis from Europe and North Africa. Character loadings on the first two principal components. Bold values indicate significant character loadings. See text for definition of variables.

Analyse morphométrique des adoralis de kirkocystidés d'Europe et d'Afrique du Nord. Scores des différentes variables sur les deux principaux axes factoriels ; les valeurs en gras sont significatives. Voir texte pour la définition des variables.

	PC1	PC2
SR	-0.632	0.674
RAH	0.943	0.222
RAL	0.608	-0.622
RAP	0.977	-0.040
RPH	0.939	0.257
RPL	-0.347	0.836
RPP	0.749	0.637
CE	-0.941	-0.218

of the variance) is mainly influenced by the posterior region of adoralis (RPP, and mostly RPL), but also by the surface ratio (SR) and the anterior region of adoralis (RAL; Table 5). Dispersal along PC2 mostly reflects intraspecific variability correlated to the asymmetry of left and right adoralis. In the case of nearly symmetrical adoralis, dispersal is low, and comparable values are observed along PC2 for both elements (e.g. *A. trapeziiformis*, *B. primus*). In the case of asymmetrical adoralis (e.g. *A. balclatchiensis*, *A. escandei*), PC2 clearly differentiates longer and narrower right elements (negative values) from broader and shorter left ones (positive values). Morphospace occupation shows that *Anatifopsis* and *Balanocystites* correspond to two continuous, juxtaposed sets (morphotypes) of adoralis. In *Anatifopsis*, adoralis exhibit a great variability both along PC1 and PC2, whereas in *Balanocystites*, their dispersal is significant along PC1, but reduced along PC2. However, if *A. escandei* is pulled out of other specimens of *Anatifopsis*, then the separation between *Anatifopsis* and *Balanocystites* becomes much more obvious, as these two genera correspond to two clearly separated, well-distinct sets of adoralis (Fig. 9). This observation suggests that the two genera can be readily identified from the morphology of their adoralis. Morphospace occupation of the 11 selected specimens (49 ontogenetic stages) of *A. escandei* is intermediate between that of other *Anatifopsis* (on the left), and that of *Balanocystites* (on the right). This situation results from the unusual morphology of adoralis belonging to this species, which have been assigned either to *Anatifopsis*, as suggested by their truncated posterior end and by the parallel courses of s_1 and s_2 (Thoral, 1935; Kobayashi, 1960; Chauvel, 1966) or to *Balanocystites*, because of their elongate and narrow morphology (Lefebvre, 1999; Vizcaïno et al., 2001). This study shows that three distinct morphotypes are present in Kirkocystidae: (1) an “*Anatifopsis* morphotype”, characterized by short and broad adoralis with a posteriorly truncated end, (2) a “*Balanocystites* morphotype”, corresponding to long and narrow adoralis with a sharp posterior extremity, and (3) an intermediate “*escandei* morphotype” with long and narrow adoralis with a truncated posterior edge.

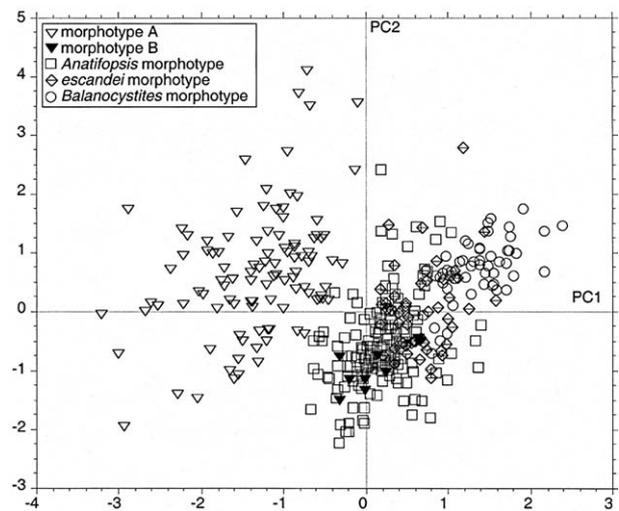


Fig. 10. Plot of morphospace occupation of 389 growth stages corresponding to 101 adoralis of European, Korean, and North African kirkocystids (Tremadocian to Caradocian) on the first two principal components.

Projection dans le plan factoriel PC1-PC2 de l'espace morphologique de 389 stades de croissance correspondant à 101 adoralis de kirkocystidés d'Europe, de Corée et d'Afrique du Nord (Trémadocien–Caradocien).

5.4. Adoralis of Korean forms vs other Kirkocystidae

The aim of this analysis is to compare morphospace occupations of the two morphotypes defined for Korean adoralis (A and B morphotypes; see above), with those of the three morphotypes evidenced within other Kirkocystidae (*Anatifopsis*, *Balanocystites*, and *escandei* morphotypes, see above).

Material and methods: This study includes all specimens and data used in the first analysis devoted to Korean adoralis (32 specimens, 114 ontogenetic stages) and in the previous one focusing on European and North African adoralis (69 specimens, 275 ontogenetic stages). Consequently, this study is based on 101 specimens, corresponding to 389 ontogenetic stages and comprising comparable proportions of left and right elements (51 and 50 specimens, respectively, corresponding to 196 and 193 ontogenetic stages, respectively). The same eight variables as in preceding analyses have been calculated for each of the 389 ontogenetic stages. This results in a very large data matrix (389 × 8), processed by PCA using Statview (version 4.51.1).

Results: PCA of eight variables extracted from 389 ontogenetic stages of Korean, European, and North African kirkocystid adoralis provides a significant result with 93.3% of the variation represented on the first two principal components (Fig. 10). PC1 and PC2 define a two-dimensional morphospace, in which the morphological diversity of Korean adoralis is expressed with a loss of 6.7% of the variation in the data set. PC1 (69.2% of the variance) is primarily influenced by the morphology of the anterior region of adoralis (RAL, RAH, and mostly RAP), but it is also influenced by the coefficient of elongation (CE; Table 6), surface ratio (SR), and posterior region (RPH). PC1 clearly discriminates adoralis with a large, inflated anterior region (on the

Table 6

Morphometric analysis of kirkocystid adoralis from Europe, Korea, and North Africa. Character loadings on the first two principal components. Bold values indicate significant character loadings. See text for definition of variables.

Analyse morphométrique des adoralis de kirkocystidés d'Europe, de Corée et d'Afrique du Nord. Scores des différentes variables sur les deux principaux axes factoriels ; les valeurs en gras sont significatives. Voir texte pour la définition des variables.

	PC1	PC2
SR	-0.869	0.330
RAH	0.880	0.377
RAL	0.897	-0.360
RAP	0.983	-0.034
RPH	0.907	0.357
RPL	-0.830	0.502
RPP	0.036	0.987
CE	-0.851	-0.434

left) from those with a narrow, reduced anterior portion (on the right). PC2 (24.1% of the variance) is related to the morphology of the posterior region of adoralis (RPL and mostly RPP; Table 6). PC2 separates adoralis with a relatively short and broad posterior region (negative values) from adoralis with a more elongate and narrower posterior portion (positive values). The high loadings observed for two variables, both on PC1 (RAP) and on PC2 (RPP), suggest that a plot comparable to that computed by multivariate analysis could be obtained by a bivariate analysis of RAP against RPP. Morphospace occupation shows that two clearly separated, sub-vertical sets of adoralis can be evidenced within kirkocystid adoralis (Fig. 10). Each of these two sets shows a great dispersal along PC2, but a more reduced variability along PC1. One of these two groups of adoralis corresponds to morphotype A of Korean forms (on the left), and the other one includes all other kirkocystid morphotypes (B, *Anatifopsis*, *escandei*, and *Balanocystites*; on the right). Korean adoralis assigned to morphotype A are characterized by a greatly inflated anterior region (negative values on PC1) and a large morphological variability of their posterior region, ranging from short and broad morphologies (negative values on PC2) to longer and narrower ones (positive values on PC2). Morphospace occupation of morphotype A adoralis is different and separated from that of the two kirkocystid genera *Anatifopsis* and *Balanocystites*. This observation suggests that these Korean adoralis should be assigned to a distinct genus. Surprisingly, the morphologic variability of morphotype A adoralis is greater than that of all other Kirkocystidae. Such a great morphological variability observed within morphotype A adoralis can be interpreted either as reflecting the co-occurrence of several species of contrasted morphology, or as an actual, large intraspecific variability possibly related to heterochronic processes (see Neige et al., 1997: Fig. 8). Morphology of morphotype A adoralis recalls the situation in primitive peltocystids (*Peltocystis*) and juvenile specimens of other kirkocystids (Fig. 4(12); see Parsley et al., 2000: Pl. 2, Fig. 7). The “juvenile” morphology of morphotype A adoralis, combined with their small size and

great morphological variability suggest that other Kirkocystidae could derive from morphotype A-like forms by peramorphosis. The second group of adoralis includes two Korean specimens (morphotype B) and all European and North African specimens (*Anatifopsis*, *escandei*, and *Balanocystites* morphotypes; Fig. 10). These adoralis are characterized by a short and narrow anterior region (slightly negative to positive values along PC1) and by a posterior region showing a wide array of possible morphology: short, broad, and posteriorly truncated (negative values along PC2; *Anatifopsis* morphotype); long, narrow, and posteriorly truncated (slightly negative to slightly positive values along PC2; *escandei* morphotype); and long, narrow, and posteriorly sharp (positive values along PC2; *Balanocystites* morphotype). Morphospace occupation of morphotype B is identical to that of the *Anatifopsis* morphotype and distinct from those of both *escandei* and *Balanocystites* morphotypes. This observation strongly supports the assignment of the two Korean specimens (9 ontogenetic stages) referred to as morphotype B, to the genus *Anatifopsis*.

5.5. Adoralis of Korean *Anatifopsis* vs other *Anatifopsis*

The aim of this morphometric analysis is to investigate the distribution of the two specimens of Korean *Anatifopsis* within the morphospace defined by the most relevant species assigned to the *Anatifopsis* morphotype.

Material and methods: This study is based on most specimens assigned to the *Anatifopsis* morphotype in previous analyses: the two adoralis of Korean *Anatifopsis* from the Tumugol Formation (nine ontogenetic stages; Fig. 4(10)), and 47 adoralis of other *Anatifopsis* (193 ontogenetic stages; Table 7). The same variables as for previous analyses have been calculated. This results in a large data matrix (202 × 8), which has been processed by PCA using Statview (version 4.51.1).

Results: PCA of eight variables calculated from 202 ontogenetic stages (49 specimens) of *Anatifopsis* provides a significant result, which groups 84.3% of the total variation on the first two factorial axes (Fig. 11). PC1 and PC2 define a two-dimensional morphospace, in which the morphological diversity of adoralis is expressed with a loss of 15.7% of the variation in the data set. PC1 (51.7% of the variance) is mostly related to the coefficient of elongation (CE) and the two relative heights (RAH, RPH), but it is also influenced by the two relative perimeters (RAP, RPP; Table 8). PC1 clearly separates short and broad adoralis (on the left) from elongate and narrower ones (on the right). PC2 (32.7% of the variance) is mostly affected by the surface ratio (SR), but also by the two relative lengths (RAL, RPL; Table 8). Consequently, PC2 mainly discriminates adoralis with a reduced, narrow anterior region (high SR, top of the diagram) from those with a relatively larger anterior region (lower SR, bottom of the diagram). Morphospace occupation shows that the various species assigned to the *Anatifopsis* morphotype can be hardly distinguished from each other based on the morphology of

Table 7

Sample sizes (specimens and ontogenetic stages) used for morphometric analysis of selected European, Korean, and North African adorals of *Anatifopsis* (Tremadocian to Caradocian). Abbreviations: A₁, left adoral; A₁, right adoral.

Nombre d'échantillons (spécimens et stades ontogénétiques) utilisés pour l'analyse morphométrique de diverses adorales d'*Anatifopsis* d'Europe, de Corée et d'Afrique du Nord (Trémadocien à Caradocien). Abréviations : A₁, adorale gauche ; A₁, adorale droite.

			Specimens			Ontogenetic stages		
			A ₁	A ₁	Total	A ₁	A ₁	Total
<i>Anatifopsis</i> sp.	Tremadocian	Korea	0	2	2	0	9	9
<i>A. trapeziiformis</i>	Tremadocian	Shropshire	3	4	7	11	15	26
<i>A. trapeziiformis</i>	L. Arenigian	Mgne Noire	11	10	21	45	44	89
<i>A. minuta</i>	Llandeilian	Brittany	1	2	3	3	8	11
<i>A. minuta</i>	Llandeilian	Morocco	3	4	7	15	18	33
<i>A. bohémica</i>	Caradocian	Bohemia	2	0	2	8	0	8
<i>A. longa</i>	Caradocian	Bohemia	0	1	1	0	3	3
<i>A. balclatchiensis</i>	Caradocian	Scotland	5	1	6	18	5	23
		Total	25	24	49	100	102	202

their adorals (Fig. 11). This observation suggests that morphology of adorals probably constitutes a useful key for genus-level identifications, but probably a less appropriate tool for species-level determinations. For example, most adorals of *A. minuta* are slightly longer and narrower than those of *A. trapeziiformis*, but adorals of *A. trapeziiformis* and *A. balclatchiensis* cannot be objectively distinguished from each other (see also Lefebvre, 1999: p. 327). Morphology of the two Korean adorals (nine ontogenetic stages) is clearly more similar to that of adorals of *A. trapeziiformis*, *A. longa*, or *A. balclatchiensis* than to that of *A. minuta* (Fig. 11). Consequently, adorals of Korean *Anatifopsis*, which cannot be objectively compared to similar elements belonging to closely related species, are maintained here in open nomenclature and referred to as *Anatifopsis* sp.

5.6. Morphotype A adorals vs *A. trapeziiformis*

The aim of this study is to compare the morphology of morphotype A adorals with that of different ontogenetic

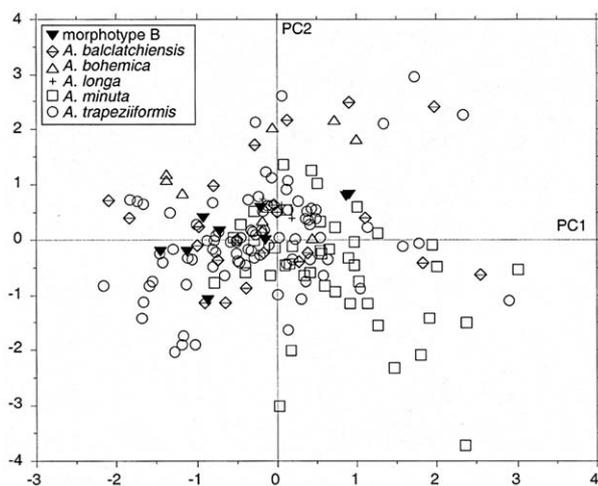


Fig. 11. Plot of morphospace occupation of 177 growth stages corresponding to 42 adorals of selected European, Korean, and North African *Anatifopsis* (Tremadocian to Caradocian) on the first two principal components. Projection dans le plan factoriel PC1-PC2 de l'espace morphologique de 177 stades ontogénétiques correspondant à 42 adorales d'*Anatifopsis* d'Europe, de Corée et d'Afrique du Nord (Trémadocien–Caradocien).

stages of similar skeletal elements in *A. trapeziiformis*, so as to investigate the possible involvement of heterochronic processes (peramorphosis) within primitive Kirkocystidae. The choice of *A. trapeziiformis* is motivated by its stratigraphic range (Tremadocian to Lower Arenigian; *A. trapeziiformis* is the oldest known kirkocystid mitrate), and the morphology of its adorals (within Kirkocystidae, the short and broad adorals of *A. trapeziiformis* are among the most similar to those of morphotype A; Fig. 4(11)).

Material and methods: This analysis is based on the same specimens of Korean adorals and *A. trapeziiformis* that have been used in the previous morphometric analyses (see above). This material represents 58 specimens (220 ontogenetic stages), including 30 adorals (105 ontogenetic stages) of morphotype A adorals from the Tumugol and Mungok formations (Tremadocian) of Korea, seven specimens (26 ontogenetic stages) of *A. trapeziiformis* from the Shington Shales (Tremadocian) of Shropshire, England, and 21 specimens of *A. trapeziiformis* (89 ontogenetic stages) from the Saint-Chinian and La Maurerie formations (Lower Arenigian) of Montagne Noire, France. The same eight variables as in the previous analyses have been calculated from 220 ontogenetic stages considered here. This results in a

Table 8

Morphometric analysis of adorals of selected European, Korean, and North African *Anatifopsis*. Character loadings on the first two principal components. Bold values indicate significant character loadings. See text for definition of variables.

Analyse morphométrique de diverses adorales d'*Anatifopsis* d'Europe, de Corée et d'Afrique du Nord. Scores des différentes variables sur les deux principaux axes factoriels ; les valeurs en gras sont significatives. Voir texte pour la définition des variables.

	PC1	PC2
SR	-0.213	0.899
RAH	0.938	-0.054
RAL	0.057	-0.807
RAP	0.862	-0.423
RPH	0.941	0.045
RPL	0.156	0.828
RPP	0.808	0.533
CE	-0.948	-0.053

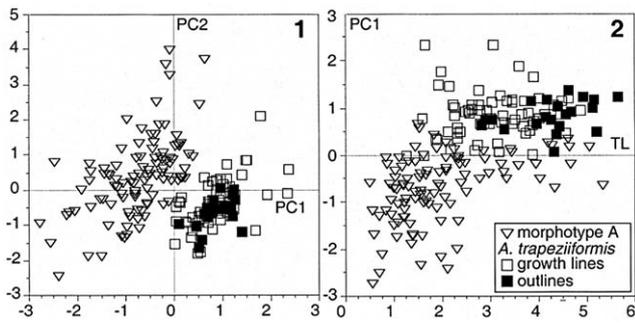


Fig. 12. Morphological comparison between morphotype A (Tremadocian, Korea) and *Anatifopsis trapeziiformis* adorals (Tremadocian, Shropshire; Lower Arenigian, Montagne Noire). **1.** Plot of morphospace occupation of 194 growth stages corresponding to 51 specimens of morphotype A adorals and *Anatifopsis trapeziiformis* on the first two principal components. **2.** Bivariate plot showing the variations of PC1 (mostly influenced by the relative anterior perimeter, RAP) during growth (expressed by the total length, TL) for morphotype A and *Anatifopsis trapeziiformis* adorals. Comparaison morphologique des adorales du morphotype A (Trémadocien de Corée) et celles d'*Anatifopsis trapeziiformis* (Trémadocien du Shropshire ; Arenig inférieur de Montagne Noire). **1.** Projection dans le plan factoriel PC1-PC2 de l'espace morphologique de 194 stades ontogénétiques correspondant à 51 adorales de type A et d'*Anatifopsis trapeziiformis*. **2.** Graphe bivariate illustrant les variations de PC1 (principalement influencé par le périmètre relatif de la région antérieure, RAP) au cours de la croissance (estimée par la longueur totale, TL), chez les adorales de type A et celles d'*Anatifopsis trapeziiformis*.

large data matrix (220 × 8), which has been processed by PCA using Statview (version 4.51.1).

Results: PCA provides a significant result, with 92.6% of the variation expressed on the first two principal components (Fig. 12(1)). PC1 and PC2 define a two-dimensional morphospace, in which the morphological diversity of adorals is expressed with a loss of 7.4% of the variation in the data set. PC1 (65.4% of the variance) is mainly influenced by the anterior region of adorals (RAL and mostly RAP), but also by the surface ratio (SR) and the posterior region (RPL; Table 9). PC1 clearly discriminates adorals with a large, inflated anterior region (on the left) from those with a narrower, reduced anterior region (on the right). PC2 (27.2% of the variance) is primarily related to the posterior region of

Table 9

Morphometric analysis of morphotype A and *Anatifopsis trapeziiformis* adorals. Character loadings on the first two principal components. Bold values indicate significant character loadings. See text for definition of variables.

Analyse morphométrique d'adorales de kirkocystidés appartenant au morphotype A et à *Anatifopsis trapeziiformis*. Scores des différentes variables sur les deux principaux axes factoriels ; les valeurs en gras sont significatives. Voir texte pour la définition des variables.

	PC1	PC2
SR	-0.880	0.344
RAH	0.802	0.472
RAL	0.904	-0.328
RAP	0.982	0.010
RPH	0.806	0.528
RPL	-0.840	0.478
RPP	-0.270	0.945
CE	-0.779	-0.569

adorals (RPH and mostly RPP), but it is also influenced by the coefficient of elongation (CE; Table 9). PC2 separates adorals with a broad and short posterior region (bottom of the diagram) from those with a longer and narrower posterior region (top of the diagram). Morphospace occupation is comparable to that obtained in the comparison of Korean, European, and North African kirkocystids, with a clear separation of morphotype A (on the left) and *A. trapeziiformis* adorals (on the right; Fig. 12(1)). Identical morphospace occupations can be evidenced for adorals of *A. trapeziiformis* from Shropshire and Montagne Noire. Distinction between the last ontogenetic stage (adoral outline) and several previous, younger ontogenetic stages (growth lines) for each adoral of *A. trapeziiformis* shows that morphological variability is clearly more reduced for adoral outlines than for growth lines (Fig. 12(1)). This observation strongly supports the view that morphological variability is greater within smaller (ontogenetically younger) specimens of *A. trapeziiformis* than in larger (“older”) ones. Reduction of morphological variability during growth can be also clearly evidenced in *A. trapeziiformis* by a simple bivariate plot of PC1 against the TL of the adoral (Fig. 12(2)): the range of possible values for PC1 is greater for younger growth stages (growth striae), than for the last observed ontogenetic stages (adoral outlines). Comparable patterns of drastic reductions of morphological variability during ontogeny have been evidenced in other invertebrates, such as cephalopods (e.g. Neige et al., 1997). A similar pattern can be also observed in morphotype A adorals (Fig. 12(2)), with a much greater morphological variability within smaller (younger) forms (TL < 2.6 mm), than for larger (older) ones (TL > 2.6 mm). Interestingly, morphology of some young ontogenetic stages of adorals in *A. trapeziiformis* is very similar to that of morphotype A adorals and especially to that of the largest (?adult) ones (TL > 2.6 mm). This morphological similarity between young growth stages of *A. trapeziiformis* and the largest observed morphotype A adorals (i.e. comparable values on PC1; Fig. 12(2)) questions the possible influence of heterochronic processes, with *Anatifopsis*-like kirkocystids deriving from morphotype A-like ancestors by peramorphosis.

Acknowledgements

This work is a contribution of the team “Macroévolution et dynamique de la biodiversité” of the UMR CNRS 5561 “Biogéosciences” and BK 21 Project (Earth and Environmental Sciences) of Seoul National University. This work has been supported by the GDR CNRS 2474 “Morphométrie et évolution des formes” and a grant from the Korea Science and Engineering Foundation (grant no. 1999-1-131-001-5). The authors are particularly grateful to J. Le Menn and C.R.C. Paul for reviewing the manuscript and making many helpful suggestions, to B. David, J.-L. Dommergues, D. Marchand, S. Montuire, P. Neige for helpful discussions on

morphometric analysis and heterochronies, to M. Ruta for correcting an early draft of the manuscript and making many constructive remarks, to J.C. Gutiérrez-Marco, R.P.S. Jefferies, J.P. Kundura, E. and S. Monceret, J. Plaine, A. Prieur, R. Prokop, S. Régnault, T. Sasaki and D. Vizcaino for the access to important specimens of kirkocystids housed in different collections, and to J.W. Sohn and I. Kang for their technical assistance during this study.

References

- Aramburu, C., Arbizu, M., Gutiérrez-Marco, J.-C., Mendez-Bedia, I., Rabano, I., Truyols, J., 1996. Primera identificación de materiales del Ordovícico Medio en la sección de Los Barrios de Luna (Zona Cantábrica, noroeste de España). *Geogaceta* 20, 7–10.
- Barrande, J., 1872. Système silurien du centre de la Bohême. Supplément au volume 1. Trilobites, crustacés divers et poissons. Rivnác, Prague.
- Barrande, J., 1887. Système silurien du centre de la Bohême, vol. 7. Classe des échinodermes, Ordre des cystidées. Rivnác, Prague; Gerhard, Leipzig.
- Bassler, R.S., 1950. New genera of American Middle Ordovician “Cystoidea”. *Washington Academy of Sciences Journal* 40, 273–277.
- Beisswenger, M., 1994. A calcichordate interpretation of the new mitrate *Eumitrocystella savilli* from the Ordovician of Morocco. *Paläontologische Zeitschrift* 68, 443–462.
- Brett, C.E., Moffat, H.A., Taylor, W.L., 1997. Echinoderm taphonomy, taphofacies, and Lagerstätten. In: Waters, J.A., Maples, C.G. (Eds.), *Geobiology of Echinoderms*. The Paleontological Society Papers 3. pp. 147–190.
- Chauvel, J., 1941. Recherches sur les cystoïdes et les carpoïdes armoricains. *Mémoires de la Société géologique et minéralogique de Bretagne* 5, 1–286.
- Chauvel, J., 1966. Présence du genre *Anatifopsis* Barrande (crustacés) dans l’Ordovicien du Maroc. *Comptes Rendus sommaires des séances de la Société Géologique de France* 8, 301–302.
- Chauvel, J., 1971. Les échinodermes carpoïdes du Paléozoïque inférieur marocain. *Notes du Service géologique du Maroc* 31, 49–60.
- Chauvel, J., 1981. Étude critique de quelques échinodermes stylophores du Massif armoricain. *Bulletin de la Société géologique et minéralogique de Bretagne* C 13, 67–101.
- Choi, D.K., 1990. *Sphenothallus* (“Vermes”) from the Tremadocian Dumugol Formation, Korea. *Journal of Paleontology* 64, 403–408.
- Choi, D.K., 1998a. The Yongwol Group (Cambrian–Ordovician) redefined: a proposal for the stratigraphic nomenclature of the Choson Supergroup. *Geosciences Journal* 2, 220–234.
- Choi, D.K., 1998b. An Early Ordovician trilobite faunule from the Choson Supergroup, Maepo, Tanyang area, Korea. *Geosciences Journal* 2, 235–242.
- Choi, D.K., Kim, K.H., 1989. Problematic fossils from the Dumugol Formation (Lower Ordovician), Dongjeom area, Korea. *Journal of the Geological Society of Korea* 25, 405–412.
- Choi, D.K., Lee, Y.I., 1988. Invertebrate fossils from the Dumugol Formation (Lower Ordovician) of Dongjeom area, Korea. *Journal of the Geological Society of Korea* 24, 289–305.
- Choi, D.K., Kim, D.H., Sohn, J.W., 2001. Ordovician trilobite faunas and depositional history of the Taebaeksan Basin, Korea: implications for palaeogeography. *Alcheringa* 25, 53–68.
- Chough, S.K., Kwon, S.T., Ree, J.H., Choi, D.K., 2000. Tectonic and sedimentary evolution of the Korean peninsula: a review and new view. *Earth-Science Reviews* 52, 175–235.
- Cripps, A.P., 1990. A new stem-craniate from the Ordovician of Morocco and the search for the sister group of the Craniata. *Zoological Journal of the Linnean Society* 100, 27–71.
- David, B., Lefebvre, B., Mooi, R., Parsley, R.L., 2000. Are homalozoans echinoderms? An answer from the extraxial-axial theory. *Paleobiology* 26, 529–555.
- Dean, W.T., 1966. The Lower Ordovician stratigraphy and trilobites of the Landeyran valley and the neighbouring district of the Montagne Noire, south-western France. *Bulletin of the British Museum (Natural History). Geology* 12, 245–353.
- Derstler, K., 1979. Biogeography of the stylophoran carpoïdes (Echinodermata). In: Gray, J., Boucot, A.J. (Eds.), *Historical Biogeography, Plate Tectonics and the Changing Environment*. Oregon State University Press, Corvallis, pp. 91–104.
- Domínguez, P., Gutiérrez, J.-C., 1990. Primeros representantes ibéricos del género *Anatifopsis* Barrande, 1872 (Homalozoa, Stylophora; Ordovícico) y su posición sistemática. *Acta Geologica Salmaticensia* 168, 121–131.
- Domínguez, P., Jacobson, A.G., Jefferies, R.P.S., 2002. Paired gill slits in a fossil with a calcite skeleton. *Nature* 417, 841–844.
- Gutiérrez-Marco, J.-C., Aramburu, C., Arbizu, M., Bernardez, E., Hacar Rodríguez, M.P., Mendez-Bedia, I., Montesinas Lopez, R., Rabano, I., Truyols, J., Villas, E., 1999. Revisión bioestratigráfica de las pizarras del Ordovícico Medio en el noroeste de España (zonas Cantábrica, Asturoccidental-leonesa y Centroibérica septentrional). *Acta Geologica Hispanica* 34, 3–87.
- Hadding, A., 1913. Undre Dicellograptusskiffern i Skåne jämte några därmed ekvivalenta bildningar. *Lunds Universitets Årsskrift* 9, 1–91.
- Jefferies, R.P.S., 1967. Some fossil chordates with echinoderm affinities. *Symposium of the Zoological Society of London* 20, 163–208.
- Jefferies, R.P.S., 1979. The origin of chordates—a methodological essay. In: House, M.R. (Ed.), *The Origin of Major Invertebrate Groups*. Systematics Association Special vol. 12. pp. 443–477.
- Jefferies, R.P.S., 1986. In: *The ancestry of the vertebrates*. British Museum (Natural History), London, pp. 1–376.
- Jefferies, R.P.S., 1987. The chordates—a preliminary note. In: Fortey, R.A., Owens, R.M. (Eds.), *The Arenig Series in South Wales: Stratigraphy and Palaeontology*. *Bulletin of the British Museum (Natural History) Geology* 41. pp. 285–290.
- Jefferies, R.P.S., Daley, P.E.J., 1996. Calcichordates. In: Harper, D.A.T., Owen, A.W. (Eds.), *Fossils of the Upper Ordovician*. *Palaeontological Association Field Guides to Fossils*, 7. pp. 268–276.
- Jones, T.R., Woodward, H., 1895. On some Palaeozoic Phyllopora. *Geological Magazine* 2, 539–545.
- Kerforne, F., 1901. Étude de la région silurique occidentale de la presqu’île de Crozon (Finistère). *Imprimerie F. Simon, Rennes*.
- Kim, K.H., Choi, D.K., Lee, C.Z., 1991. Trilobite biostratigraphy of the Dumugol Formation (Lower Ordovician) of Dongjeom area, Korea. *Journal of the Paleontological Society of Korea* 7, 106–115.
- Kobayashi, T., 1934. The Cambro-Ordovician formations and faunas of South Chosen. *Palaeontology*. Part 2, Lower Ordovician faunas. *Journal of the Faculty of Science, Imperial University of Tokyo* 3, 521–585.
- Kobayashi, T., 1960. The Cambro-Ordovician formations and faunas of South Korea. Part 6. *Palaeontology* 5. *Journal of the Faculty of Science, University of Tokyo Section 2* 12, 217–275.
- Kobayashi, T., 1966. The Cambro-Ordovician formations and faunas of South Korea, Part 10, Stratigraphy of the Chosen Group in Korea and South Manchuria and its relation to the Cambro-Ordovician formations of other areas, Section A, The Chosen Group of South Korea. *Journal of the Faculty of Science, University of Tokyo* 16, 1–84.
- Kobayashi, T., Yosimura, I., Iwaya, Y., Hukasawa, T., 1942. The Yokusen Geosyncline in the Chosen period. Brief notes on the geologic history of the Yokusen orogenic zone. *Proceedings of Imperial Academy of Tokyo* 18, 579–584.
- Kolata, D.R., Frest, T.J., Mapes, R.H., 1991. The youngest carpoïd: occurrence, affinities and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. *Journal of Paleontology* 65, 844–855.
- Kwon, Y.K., Chough, S.K., Choi, D.K., Lee, D.J., 2002. Origin of limestone conglomerates in the Choson Supergroup (Cambro-Ordovician), mid-east Korea. *Sedimentary Geology* 146, 265–283.

- Lee, Y.I., Kim, J.C., 1992. Storm-influenced siliciclastic and carbonate ramp deposits, the Lower Ordovician Dumugol Formation, South Korea. *Sedimentology* 39, 951–969.
- Lefebvre, B., 1999. Stylophores (Cornuta, Mitrata): situation au sein du phylum des échinodermes et phylogénèse. Thèse de doctorat, Université Claude Bernard Lyon-1 (inédit).
- Lefebvre, B., 2000a. Les échinodermes stylophores du Massif armoricain. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France* 22, 101–122.
- Lefebvre, B., 2000b. A new mitrate (Echinodermata, Stylophora) from the Tremadoc of Shropshire (England) and the origin of the Mitrocystitida. *Journal of Paleontology* 74, 890–906.
- Lefebvre, B., 2001. A critical comment on “ankyroids” (Echinodermata, Stylophora). *Geobios* 34, 597–627.
- Lefebvre, B., 2003. Functional morphology of stylophoran echinoderms. *Palaeontology* 46, 511–555.
- Le Goarant de Tromelin, G., Lebesconte, P., 1876. Essai d'un catalogue raisonné des fossiles siluriens des départements de Maine-et-Loire, de la Loire-inférieure et du Morbihan, avec des observations sur les terrains paléozoïques de l'Ouest de la France. In: *Comptes Rendus de l'Association française pour l'Avenir des Sciences*, 4e session. Nantes 1875. pp. 601–661.
- McGhee, G.R., 1999. *Theoretical Morphology. The Concept and its Applications*. Columbia University Press, New York.
- Neige, P., Marchand, D., Laurin, B., 1997. Heterochronic differentiation of sexual dimorphs among Jurassic ammonite species. *Lethaia* 30, 145–155.
- Nichols, D., 1972. The water-vascular system in living and fossil echinoderms. *Palaeontology* 15, 519–538.
- Parsley, R.L., 1982. Functional morphology of mitrate homalozoans (Echinodermata). *Geological Society of America, Abstracts with Programs* 14, 583.
- Parsley, R.L., 1988. Feeding and respiratory strategies in Stylophora. In: Paul, C.R.C., Smith, A.B. (Eds.), *Echinoderms Phylogeny and Evolutionary Biology*. Clarendon Press, Oxford, pp. 347–361.
- Parsley, R.L., 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). *Bulletins of American Paleontology* 100, 5–57.
- Parsley, R.L., Prokop, R.J., Derstler, K., 2000. Kirkocystid ankyroids (Stylophora: Echinodermata) from the Sarka Formation (Ordovician) of Bohemia. *Vestník Českého geologického ústavu* 75, 37–47.
- Philip, G.M., 1979. Carpoids: echinoderms or chordates? *Biological Reviews of the Cambridge Philosophical Society* 54, 439–471.
- Pillet, J., Beaulieu, G., 1998. Sur quelques espèces rares des «Schistes d'Angers» (Llandeilou et Caradoc). *Bulletin de la Société d'Études Scientifiques de l'Anjou* 16, 161–174.
- Pope, J., 1975. Evidence for relating the Lepidocoleidae, maechaeridian echinoderms to the mitrate carpoids. *Bulletins of American Paleontology* 67, 385–406.
- Reed, F.R.C., 1907. Crustacea, etc., from Girvan. *Geological Magazine* 4, 108–115.
- Regnell, G., 1945. Non-crinoid Pelmatozoa from the Paleozoic of Sweden. *Meddelanden från Lunds Geologisk-Mineralogiska Institution* 108, 1–255.
- Rolfé, W.D.I., 1969. Phyllocarida. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, part R, Arthropoda* 4(1). Geological Society of America and University of Kansas Press, Boulder, CO; Lawrence, KS, pp. R296–R331.
- Seo, K.S., Lee, H.Y., Ethington, R.L., 1994. Early Ordovician conodonts from the Dumugol Formation in the Baegunsan Syncline, eastern Yeongweol and Samcheog areas, Kangweon-do, Korea. *Journal of Paleontology* 68, 599–616.
- Spencer, W.K., 1950. Asterozoa and the study of Palaeozoic faunas. *Geological Magazine* 87, 393–408.
- Sprinkle, J., Guensburg, T.E., 1995. Origin of echinoderms in the Paleozoic evolutionary fauna: the role of substrates. *Palaios* 5, 437–453.
- Thoral, M., 1935. Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire. Imprimerie de la Charité, Montpellier.
- Ubahgs, G., 1961. Sur la nature de l'organe appelé tige ou pédoncule chez les «carpoïdes» Cornuta et Mitrata. *Comptes Rendus des séances de l'Académie des Sciences* 253, 2738–2740.
- Ubahgs, G., 1967. Stylophora. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, part S, Echinodermata* 1(2). Geological Society of America and University of Kansas Press, Boulder, CO; Lawrence, KS, pp. 495–565.
- Ubahgs, G., 1969. Les échinodermes «carpoïdes» de l'Ordovicien inférieur de la Montagne Noire (France). *Cahiers de Paléontologie*. Éditions du CNRS, Paris.
- Ubahgs, G., 1979. Trois Mitrata (Echinodermata: Stylophora) nouveaux de l'Ordovicien de Tchécoslovaquie. *Paläontologische Zeitschrift* 53, 98–119.
- Ubahgs, G., 1981. Réflexions sur la nature et la fonction de l'appendice articulé des «carpoïdes» Stylophora (Echinodermata). *Annales de Paléontologie (Invertébrés)* 67, 33–48.
- Vizcaïno, D., Lefebvre, B., 1999. Les échinodermes du Paléozoïque inférieur de Montagne Noire: biostratigraphie et paléodiversité. *Geobios* 32, 353–364.
- Vizcaïno, D., Álvaro, J.J., Lefebvre, B., 2001. The Lower Ordovician of the southern Montagne Noire. *Annales de la Société Géologique du Nord* 8, 213–220.
- Withers, T.H., 1926. *Catalogue of the Machaeridia*. British Museum (Natural History), London, pp. 1–99.
- Zhou, Z., Fortey, R.A., 1986. Ordovician trilobites from North and North-eastern China. *Palaeontographica Abteilung A* 192, 157–210.