

# ORIGIN AND EVOLUTION OF THE CRETACEOUS MICROMORPH AMMONITE FAMILY FLICKIIDAE

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**ABSTRACT.** The ammonite family Flickiidae is a mid-Cretaceous (Albian-Cenomanian) dwarf (3 cm or less diameter) group of three genera, *Flickia* Pervinquier, 1907, *Ficheuria* Pervinquier, 1910, and *Adkinsia* Böse, 1928 to which *Salaziceras* Breistroffer, 1936 is here added, characterized by the evolution of an archetypal simplified suture and shell form closely homoeomorphic of the ancestral Devonian Anarcestina. Previously regarded as cryptogenic, the family is shown to be an offshoot of *Neophlycticeras* of the Stoliczkaiinae with simplifying suture. *F. kiltani* (Pervinquier) is a paedomorphic derivative of *S. salazacense* (Hébert and Munier-Chalmas) characterized by small size, globose simple shell and only slightly incised sutures. It gave rise to forms with progressively fewer incisions in lobes and saddles, and eventually to some with entire sutural elements. From these arose the sparsely ribbed and bullate endemic North American *Adkinsia* and the more widely occurring compressed, evolute, smooth to ribbed *Flickia*.

THE Flickiidae Adkins, 1928 is one of the few Mesozoic families of Ammonitina that includes genera showing a return to the simple entire lobes and saddles of the earliest ammonoids. These Cretaceous (Albian-Cenomanian) ammonites more closely resemble Devonian ammonoids than any of their contemporaries. The first member of the group to be described was the genus *Flickia* Pervinquier, 1907, with type species *F. simplex* Pervinquier (1907, p. 212, pl. 9, figs. 2a-b, 3a-b, 4, 5a-b; text-figs. 80, 82), a group of small (5-15 mm diameter) fairly evolute compressed smooth ammonites with narrow, arched venters, initially described from the Lower Cenomanian pyritic marls of north and central Tunisia. Pervinquier compared his specimens to Triassic ceratites such as *Nannites* Mojsisovics, 1881 and *Lecanites* Mojsisovics, 1882 as well as the Cenomanian *Neolobites* Fisher, 1882. He considered the possibility that they might be juveniles of the latter genus (which has entire, prolecanitid-like lobes and saddles), but was able to dismiss this on the basis of the fewer sutural elements of *Flickia* and the quite different shell form. He did, however, place it close to *Neolobites* within the hoplitids.

In 1920, W. S. Adkins described two further species from similar pyritic clays in Texas, *F. boesei* (Adkins) (1920, p. 85, pl. 1, figs. 1-3) and *F. (?) bosquensis* Adkins (1920, p. 87, pl. 1, fig. 4). The latter, with prominent umbilical bullae, Adkins believed to represent a new genus, and Böse (1928, p. 232) named it *Adkinsia*, with *A. adkinsi* Böse (1928, p. 237, pl. 8, figs. 9-14) as type species, also referring to it *A. bosquensis* (Adkins), *A. sparsicosta* Böse (1928, p. 238, pl. 8, figs. 15-20), *A. tuberculata* Böse (1928, p. 240, pl. 8, figs. 21-26), and *A. semiplicata* Böse (1928, p. 246, pl. 9, figs. 7-12).

With the description of the rich faunas from pyritic clays in Madagascar, Collignon (1928-1929, 1931, 1964) added further species of these rare ammonites, including *F. pervinquieri* Collignon (1929, p. 4, pl. 2, figs. 15, 15a; text-fig. 14), *F. costellata* Collignon (1964, p. 23, pl. 322, fig. 1427), and *F. quadrata* Collignon (1964, p. 23, pl. 322, figs. 1428-1429). The affinities of the group have remained an enigma; apart

from Pervinquier's suggestion that they might be hoplitids, Böse suggested a possible relationship to *Douvilleiceras*, and in the *Osnovy* (Orlov, ed., 1958) they were attached to the Binneyitidae.

In 1952 Wright (p. 219 n. 17) suggested that the Flickiidae (taken to include *Flickia* and *Adkinsia*) might be referred to the Desmocerataceae, but in 1957 (p. L409) drew analogies with the early smooth whorls of *Mojsisovicsia* Steinmann, 1881 and *Falliceras* Parona and Bonarelli, 1897 (see Kennedy and Cooper, 1977) to suggest a provisional placement in the Acanthocerataceae, between the Brancoceratidae and Lyelliceratidae, adding at this time the genus *Ficheuria* Pervinquier, 1910 to the family.

We would now argue that it is in this last genus, originally described as a possible degenerate desmoceratid, that the origins of the group are to be traced, and that the family is linked to *Neophlyticeras* Spath, 1921 of the family Lyelliceratidae by way of *Salaziceras* Breistroffer, 1936 (type species *Ammonites salazacensis* Hébert and Munier-Chalmas, 1875).

A brief systematic survey and illustration of the species referred to *Salaziceras*, *Ficheuria*, *Flickia*, and *Adkinsia* is provided below, on the basis of which the evolution of the group is outlined.

#### SYSTEMATIC PALAEOLOGY

##### Family FLICKIIDAE Adkins, 1928

##### Genus SALAZICERAS Breistroffer, 1936, p. 64

(= *Salaziceras* Breistroffer, 1940, p. 57, illegitimate emendation)

*Type species.* *Ammonites salazacensis* Hébert and Munier-Chalmas 1875, p. 114, pl. 5, fig. 6, by original designation.

*Diagnosis.* Small, rarely exceeding 30 mm in diameter, inflated, moderately involute with a deep conical umbilicus. Whorl section depressed, reniform. Ornament consists of weak to strong umbilical bullae giving rise to single or paired coarse rounded more or less straight ribs which may loop to umbilical bullae on the opposed flank or terminate as intercalatories.

Suture with much simplified E and L; L/U<sub>2</sub> bifid with only minor incisions.

*Occurrence.* *Salaziceras* at the type locality, Salzac, Gard, France, occurs with a fauna indicating the lower part of the *Stoliczkaia dispar* Zone, the *S. (Faraudiella) gardonica* Subzone of Breistroffer (e.g. 1940) and others. The same age is suggested by a previously unnoticed Cambridge Greensand example (BMNH C81310 ex. L. F. Spath Collection). Elsewhere, the genus is dated no more closely than *dispar* Zone, being recorded from the Bakony Mountains of Hungary (Nagy 1971) the Tarfaya Basin in Morocco (Wiedmann in Förster 1978 p. 158), and Nigeria (Förster, 1978).

*Discussion.* Only the type species has been referred to *Salaziceras*, which stands apart from its contemporaries. There is a superficial resemblance to the much earlier genera *Brancoceras* Steinmann, 1881 and *Hysterocheras* Hyatt, 1900 (indeed, Haug 1911 referred the type species to the former). These are, however, mere heterochronous homoeomorphs. *Salaziceras* is better regarded as a paedomorphic derivative of Lyelliceratidae. Breistroffer (1940) suggested that it arose from contemporary *Stoliczkaia*; this derivation was accepted by Spath (1923–1943), Wright (1957), and Schindewolf (1966), as several members of the family show sutural simplification, although none other to the degree shown in *Salaziceras*. However, the general form

of the genus is much closer to *Neophlycticeras* of the *brottianum* (d'Orbigny) group (see Pl. 1, figs. 1-2) than to any *Stoliczkaia* and we regard this as the most probable ancestry. Since *Salaziceras* is already dwarfed and has a very simple suture it is in our view better placed in the Flickiidae than Lyelliceratidae.

The name of the genus was originally published as *Salaziceras* (Breistroffer 1936, p. 64). Subsequently Breistroffer (1940, p. 57 n. 53) stated that this was a typographic error and corrected the name to *Salazaceras*. Under the Rules (*Code*, Article 32 (a) (ii)) this is an illegitimate emendation, since in the original publication there was no evidence of inadvertent error.

*Salaziceras salazacensis* (Hébert and Munier-Chalmas)

Plate 87, figs. 3-9; text-figs. 1a-h, 3a-c

- 1875 *Ammonites salazacensis* Hébert and Munier-Chalmas, p. 114, pl. 5, fig. 6.  
 1911 *Brancoeras salazacensis* (Hébert and Munier-Chalmas); Haug, p. 1253.  
 1936 *Salaziceras salazacensis* (Hébert and Munier-Chalmas); Breistroffer, p. 64.  
 1940 *Salaziceras salazacensis* (Hébert and Munier-Chalmas); Breistroffer, p. 57.  
 1957 *Salaziceras salazacensis* (Hébert and Munier-Chalmas); Wright, p. L410, fig. 530, 2.  
 1966 *Salaziceras salazacensis* (Hébert and Munier-Chalmas); Schindewolf, p. 791, text-fig. 437a-f.  
 1971 *Salaziceras* sp., Nagy, p. 28, pl. 4, figs. 9-10.

*Types.* Hébert and Munier-Chalmas figured only one specimen of their new form, and this specimen, preserved in the Collections of the Sorbonne (now in the Université Paris VI), and from 'près de Salazac, vallon de Cabarresse dans la Craie à Fossiles de Rouen' is taken as the holotype of the species by monotypy. A cast is preserved in the Sedgwick Museum, Cambridge.

*Other specimens studied.* Numerous topotype examples in the Collections of the Department of Geology, Grenoble, Sorbonne (now Université Paris VI) and Wright's Collection. A single Cambridge Greensand specimen, BMNH C81310.

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype <sup>1</sup>	24.0(100)	11.0(46)	9.0(38)	1.22	7.0(29)
Example 1 <sup>2</sup>	28.0(100)	12.5(45)	10.5(38)	1.19	9.0(32)
Example 2 <sup>2</sup>	23.0(100)	10.5(46)	9.5(41)	1.11	7.0(30)
Wright's Coll. F218	24.5(100)	13.1(53)	10.5(43)	1.24	6.2(25)
Wright's Coll. F219	21.0(100)	12.3(58)	8.9(42)	1.38	5.2(25)
EMP <sup>3</sup>	16.3(100)	10.1(61)	8.2(50)	1.23	3.8(23)

All measurements are in millimetres; figures in parentheses are dimensions as a percentage of total diameter. *D* = diameter, *Wb* = whorl breadth, *Wh* = whorl height, *U* = umbilicus. 1—after Hébert and Munier-Chalmas. 2—after Breistroffer. 3—École des Mines, Paris.

*Description.* Coiling is moderately involute, the shell being subglobose, with a deep conical umbilicus, the wall of which is flattened and markedly inclined outwards. It tends to widen at maturity, the seam being excentric and coiling slightly scaphitoid. The whorl section is depressed (see table of measurements), reniform, with the greatest breadth at the umbilical bullae, the flanks swollen and merging with the broadly rounded venter.

The outer whorl typically bears twenty ribs per whorl, the inner whorls somewhat fewer. There are eight strong bullae, which give rise to one or two strong rounded ribs. These are straight or feebly convex, slightly rursiradial, and markedly thickened across the venter, where they are separated by slightly wider, deep interspaces. Ribs may loop from the bulla on one flank to that on the other, or may simply end at mid-flank

on the further side as an intercalatory. There are, in addition, occasional long, non-bullate ribs and intercalatories. The ribbing may be gently flexed, concave across the flanks and convex on the venter, although this tends to be less marked on the body chamber.

Suture line very simple, with a broad E, narrower, little divided L and simplified  $U_2$ . E/L is broad and bifid with minor incisions, L/ $U_2$  smaller and also bifid with only one minor median incision.

*Occurrence.* Upper Albian, lower part of the *Stoliczkaia dispar* Zone, (*S. (Faraudiella) gardonica* Subzone of authors) of Salazac (Gard); condensed *S. dispar* Zone, Glauconitic, and Turrilitic Marls of the Bakony Mountains, Hungary; Cambridge Greensand, Cambridge, England.

*Discussion.* Nagy's (1971, p. 28, pl. 4, figs. 9–10) material, referred to as *Salaziceras* sp., has ribs arising in pairs from umbilical bullae, a feature also shown by topotypes before us. Breistroffer (1940, p. 58) described but did not name a variant, represented by three specimens in the Toucas Collection, in which the whorl section was much wider than high in the juvenile, resembling *Sonneratia dutempleana* (d'Orbigny).

#### Genus FICHEURIA Pervinquier, 1907

*Type species.* *Ficheuria kiliani* Pervinquier, 1910, p. 35, by monotypy.

*Diagnosis.* Small, very involute, globular with deep conical umbilicus and angular shoulder. Early whorls smooth, or with sparse shallow constrictions. The body chamber may bear transverse irregular ribs and folds. Suture simple, with slightly incised or entire lobes and saddles.

*Occurrence.* *Ficheuria* occurs in the uppermost Albian or basal Cenomanian of Algeria, Texas, and Mexico, and the probable early Cenomanian of Japan (Hokkaido). Nagy (1971) records it also from the Upper Albian of Hungary.

*Discussion.* *Ficheuria* represents the next stage in reduction of ornament and simplification of sutures after *Salaziceras*, but still shows, in its shape and (where present) adult ribbing, distinct resemblances to that genus. It differs from *Adkinsia* in retaining some minor incisions of the sutural elements and in over-all shell form, as well as lacking strong ribs and bullae. *Flickia* are evolute, usually high-whorled rather than globose, and have entire lobes and saddles.

Several species are described below, mainly based on single specimens of phragmocones, and distinguished on details of whorl section and suture line. With abundant material it might be that some species will prove to be synonyms.

#### *Ficheuria kiliani* Pervinquier

Plate 87, figs. 16–19, 21–26; text-figs. 1a–b, 3e–g

- 1866 *Ceratites* sp. n. Peron, p. 692.
- 1910 *Ficheuria kiliani* Pervinquier, p. 36, pl. 3, figs. 9–10; text-figs. 16–17.
- 1925 *Ficheuria kiliani* Pervinquier; Diener, p. 215.
- 1938 *Ficheuria kiliani* Pervinquier; Roman, p. 419, text-fig. 49A–B.
- 1971 *Ficheuria kiliani* Pervinquier; Nagy, p. 27, pl. 4, figs. 3–4.
- 1975 *Ficheuria kiliani* Pervinquier; Matsumoto and Inoma, p. 291.

*Types.* This species was based on three specimens; the holotype is the original of Pervinquier 1910, pl. 3, figs. 9a–d, from Sidi Ali (Djebel Guessa), Tunisia. The figured paratype (Pervinquier, 1910, pl. 3, figs. 10a–b) is from the same locality, and both specimens are preserved in the Sorbonne Collections, now at the Université Paris VI. We have been unable to locate the second paratype mentioned by Pervinquier, a crushed individual in the Thomas Collection from Berrouaghia, Algeria.

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	17.2(100)	8.6(50)	6.3(37)	1.36	3.3(19)
at	13.3(100)	—(—)	5.5(41)	—	2.8(21)

*Description.* Both specimens are pyritic internal moulds, the holotype having half a whorl of body chamber preserved and appearing adult; the paratype is crushed with approximately one quarter of a whorl of body chamber preserved. The shell is globose, with a depressed, reniform whorl section (whorl) breadth to height ratio is up to 1.36. The coiling is very involute, with a deep conical umbilicus, the wall of which slopes outwards to the abrupt and narrowly rounded umbilical shoulder.

The phragmocone is smooth, but on the slightly scaphitoid body chamber, there are low, flat, ribbon-like, faintly flexuous prorsiradiate ribs separated by weakly constricted interspaces.

The sutures are the most complex seen in the genus. E is narrow and deep with a small median element, E/L broad and asymmetrically bifid with minor denticulation. L is narrow with a series of minor incisions at the base, L/U<sub>2</sub> plump and bifid, U<sub>2</sub> small with two minor frills. U<sub>2</sub>/U<sub>3</sub> is smaller and feebly bifid.

*Occurrence.* 'Upper Albian' of Algeria, Tunisia; *dispar* Zone of the Bakony Mountains, Hungary.

*Discussion.* No other species has lobes and saddles subdivided to the degree shown in *F. kiliani*. *F. pernoni* Dubourdieu (1953, p. 35, pl. 3, figs. 51–54; text-fig. 11) has only a few incisions in the saddles and an entire L, and is more depressed with a sharper umbilical shoulder. *F. aff. pernoni* (see below) has an even simpler suture. *F. pusilla* Matsumoto and Inoma (1975, p. 290, pl. 42, figs. 4–5; text-figs. 15–16) has entire lobes and saddles in the suture and stronger ribs on the body chamber. *F. rudelli* (Dubourdieu) (1949, in Dubourdieu and Sigal, p. 214, pl. 6, figs. 1–3; text-figs. 1–2) has a much steeper umbilical wall, angular shoulder, and entire lobes and saddles.

*Ficheuria pernoni* Dubourdieu

Text-figs. 1c, 3h

1953 *Ficheuria pernoni* Dubourdieu, p. 35, pl. 3, figs. 51–54; text-fig. 11.1975 *Ficheuria pernoni* Dubourdieu; Matsumoto and Inoma, p. 291.

*Holotype.* By monotypy, Dubourdieu's original specimen from the uppermost Albian (niveau F of Durboudieu) of Henchir el Kerkour, west of Djebel Ouenza in the Monts du Mellègue, Algeria.

*Description.* The holotype is a crushed and distorted wholly septate pyritic internal mould, only 10 mm in diameter. The shell is globose, very involute, with a deep, narrow conical umbilicus with a steeply inclined umbilical wall, abrupt, subangular umbilical shoulder and depressed almost semi-circular whorl section. The shell is smooth, except for a faint, straight, prorsiradiate constriction at the end of the last preserved part of the phragmocone.

The suture (text-fig. 1c) is very simple, with a tall E with an entire median element. E/L is tall, with minor incisions, L broad, shallow, and entire. L/U<sub>2</sub> is small and low, with minor, shallow incisions.

*Occurrence.* *F. pernoni* is only known from the type occurrence, in the uppermost Albian of Algeria.

*Discussion.* Although based on a single specimen, *F. pernoni* is easily distinguished from other species referred to the genus. *F. kiliani* has a much less depressed whorl section, with a much less acute umbilical shoulder and lower expansion rate, whilst the elements of the suture have more minor incisions.

*F. pusilla* has a simpler suture with saddles entire throughout growth, as does *F. rudelli* Dubourdieu.

*Ficheuria* aff. *pernoni* (Dubourdieu)

Plate 87, figs. 14–15, 20; text-fig. 1d

*Material.* A specimen in the late J. P. Conlin's Collection, from the basal Paw Paw Formation (Upper Albian), Sycamore Creek, Fort Worth, Tarrant County, Texas, and a second, unregistered specimen in the U.S. National Museum, Washington D.C., and from the same Formation,  $\frac{7}{8}$  mile east of Watagua Texas' (Renfro Collection).

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
USNM, Renfro Coll.	7.3(100)	5.2(71)	3.2(44)	1.62	0.9(12)

*Occurrence.* Upper Albian, Paw Paw Formation, Texas.

*Discussion.* These two specimens closely resemble *F. pernoni*, differing, however, in having E/L divided by a minor incision and L/U<sub>2</sub> entire, rather than crenulated as in Dubourdieu's species.

*Ficheuria pusilla* Matsumoto and Inoma

Plate 87, figs. 10–13; text-figs. 1f, 3i

1975 *Ficheuria pusilla* Matsumoto and Inoma, p. 290, pl. 42, figs. 4–5; text-figs. 15–16.

*Types.* The holotype, no 30603 and paratypes 30168A–B are in the Collections of the Department of Geology, Kyushu University, and are all from the uppermost Albian or lowest Cenomanian of the Shumarinai River, Hokkaido, Japan.

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype, K.U. 30603	15.0(100)	8.5(56)	6.5(43)	1.3	—
Paratype, K.U. 30168A	13.0(100)	7.0(54)	5.4(42)	1.3	3.5(27)

*Occurrence.* The type occurrences are not conclusively dated, but are close to, and probably just above the Albian/Cenomanian boundary.

## EXPLANATION OF PLATE 87

Figs. 1–2. *Neophlycticeras brottianum* (d'Orbigny), MNHP 5757 (d'Orbigny Collection), the holotype from the Albian of Perte du Rhône, France.

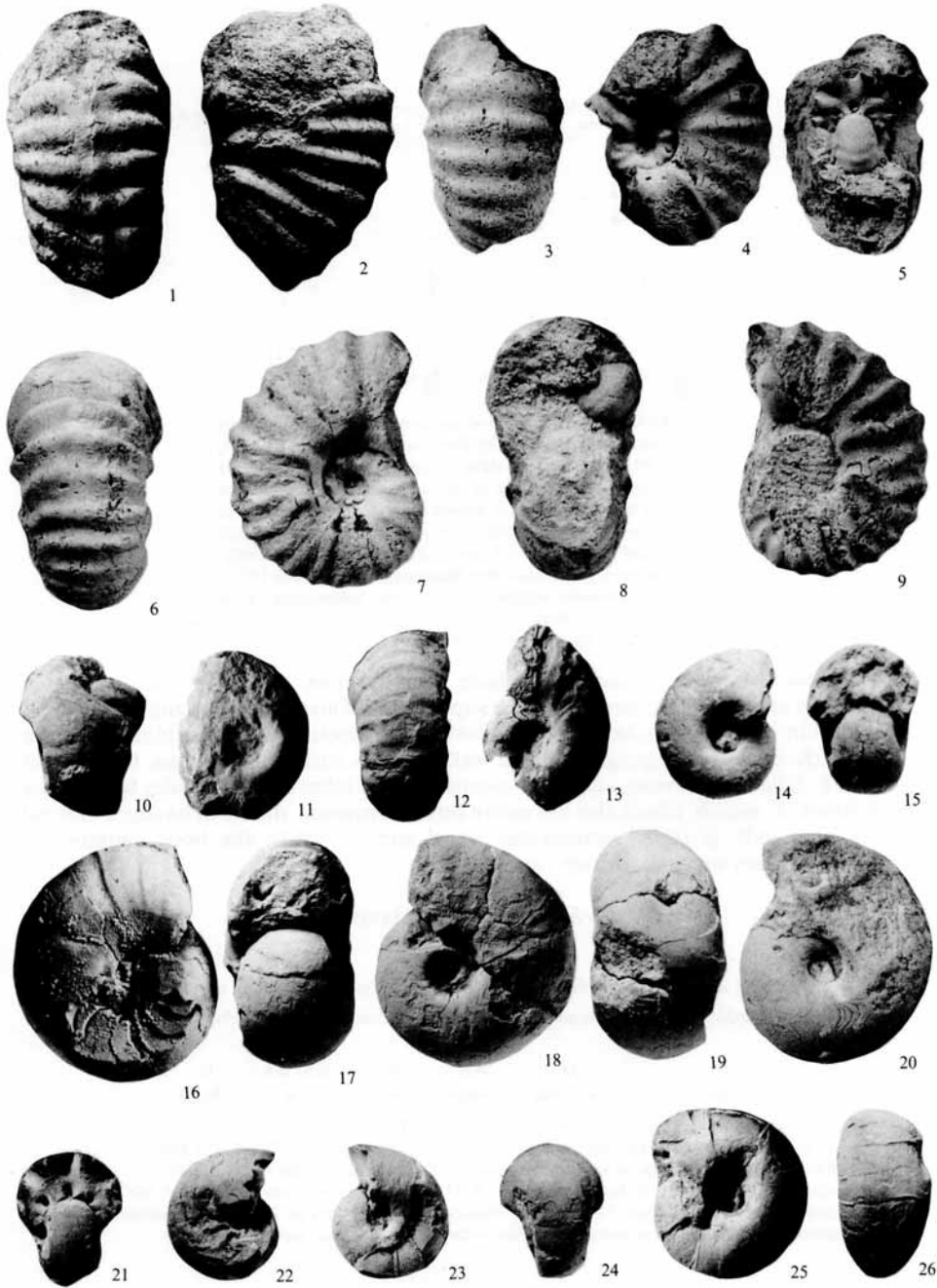
Figs. 3–9. *Salaziceras salazacense* (Hébert and Munier-Chalmas), two topotypes, WW F.218–219, from the Upper Albian of Salazac, Gard, France.

Figs. 10–13. *Ficheuria pusilla* Matsumoto and Inoma. 10–11 a paratype, Kyushu University Collections no. KU 30168A. 12–13 the holotype, KU 30603, from the uppermost Albian or Lower Cenomanian of the Shumarinai River, Hokkaido, Japan.

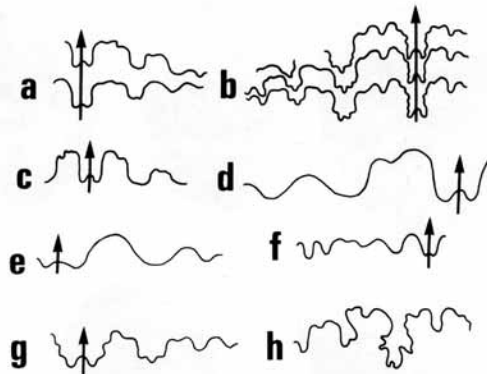
Figs. 14–15, 20. *Ficheuria* aff. *pernoni* (Dubourdieu). 14–15, an unregistered specimen in the collections of the U.S. National Museum, Washington D.C., from the Paw Paw Formation (Upper Albian),  $\frac{7}{8}$  mile east of Watagua, Texas' (Renfro Collection). 20, a specimen in the late J. P. Conlin's Collection, from the same horizon on Sycamore Creek, Tarrant County, Texas.

Figs. 16–19, 21–26. *Ficheuria kiliani* (Perinquierère). 16–19, 21–24, the holotype, and 25–26 a paratype, from the Upper Albian of Sidi Ali (Djebel Guessa), Tunisia, in the Sorbonne Collections, Paris.

Figs. 1–2 are  $\times 1$ , the remainder are  $\times 2$ .



WRIGHT and KENNEDY, Ammonite family Flickiidae



TEXT-FIG. 1. *a*, Last two sutures of the paratype of *Ficheuria kiliani* figured by Pervinquier (1907) as his pl. 3, fig. 10.  $\times 3$ . *b*, Last three sutures of the holotype of *F. kiliani*.  $\times 6$ . *c*, Suture of the holotype of *F. pernoni* at a whorl height of 6 mm. *d*, Suture of the Conlin specimen of *F. aff. pernoni*.  $\times 3$ . *e*, Suture of *F. rudelli* (Dubourdieu) at a whorl height of 4.5 mm (after Dubourdieu 1949). *f*, Suture of *F. pusilla* (after Matsumoto and Inoma 1975).  $\times 3$ . *g*, Juvenile suture of *Salaziceras salazacense* (after Schindewolf 1966). *h*, Mature suture of *S. salazacense*, after a specimen in the Wright's Collection.  $\times 3$ .

*Discussion.* Matsumoto and Inoma have recently given a very full description of *F. pusilla* and repetition here would be superfluous. This species has entire lobes and saddles in the suture, a depressed, reniform whorl section and an umbilicus with a distinctly outwards-sloping umbilical wall. Sutures easily differentiate this species from *F. kiliani*, *F. pernoni*, and *F. aff. pernoni*, where lobes and/or saddles have minor incisions. *F. rudelli*, which also has entire sutural elements, differs in having a vertical umbilical wall, giving a semicircular whorl section, whilst the body chamber of *F. pusilla* bears stronger, denser ribs and folds.

#### *Ficheuria rudelli* (Dubourdieu)

Text-fig. 1e

1949 *Flickia rudelli* Dubourdieu in Dubourdieu and Sigal, p. 214, pl. 6, figs. 1-3; text-figs. 1-2.

*Holotype.* Dubourdieu's original specimen, from the Lower Cenomanian of Djebel Ouenza, Algeria.

#### *Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	11.2(100)	7.6(68)	4.0(36)	1.9	4.8(43)

*Description.* The holotype and only known specimen is a well-preserved internal mould with two thirds of a whorl of body chamber preserved, the last few sutures being approximated. The shell is globose, with a wide, deep umbilicus with a sub-vertical wall and angular umbilical shoulder. The whorl section is very depressed, semicircular, with a breadth to height ratio of 1.9. The phragmocone is smooth, except for two or three weak prorsiradiate constrictions. On the body chamber, there are four or five low prorsiradiate folds and depressions, which produce an undulose profile to the venter in lateral view.



The adult suture is very simple, with a very broad E with a shallow median element, broad entire E/L, L, and U<sub>2</sub>.

*Occurrence.* Lower Cenomanian of Djebel Ouenza, Algeria.

*Discussion.* *F. rudelli* was originally referred to *Flickia* by Dubourdieu, but the combination of shell form, whorl section and suture place it closest to *Ficheuria*. This species comes from the same locality as *F. pernoni*, but the two can be separated by the narrower umbilicus and minor incisions in E/L and L/U<sub>2</sub> of the latter.

*F. kiliani* has a quite different shell form and coiling, and its adult sutures show minor incisions in both lobes and saddles.

*F. pusilla* has similarly entire lobes and saddles in the suture, and appears to be a Japanese analogue of the North African species. It has, however, a less depressed whorl section, outwards sloping rather than vertical wall to the smaller umbilicus, and stronger, more numerous radial ribs and folds on the body chamber.

### Genus FLICKIA Pervinquière, 1907

*Type species.* *Flickia simplex* Pervinquière, 1907 by monotypy.

*Diagnosis.* Small, moderately involute to evolute, compressed, with small to large umbilicus. Whorl sides flattened, venter rounded to fastigiata. Shell smooth, or ornamented by fine flexuous striae on the phragmocone which strengthen into flexuous ribs or irregular folds and constrictions on the body chamber, being most marked across the venter.

Suture simple, with entire lobes and saddles.

*Occurrence.* *Flickia* occurs in the Upper Albian Paw Paw Formation of Texas and in the basal Cenomanian in North Africa, Tanzania, Madagascar, and Zululand.

*Discussion.* *Flickia* differs from *Ficheuria* such as *F. kiliani* and *F. pernoni* in having entire lobes and saddles, and can be separated from all species on the basis of compressed rather than depressed whorls, and shallow rather than deep umbilicus with low, rather than high wall and rounded rather than angular shoulders. It differs from *Adkinsia* in lacking strong umbilical folds or bulges, being less inflated with a narrowly arched venter and a shallower umbilicus with a more angular shoulder. As in the case of *Ficheuria*, some of the described species of *Flickia* may prove to be synonyms when more material is known.

### *Flickia simplex* Pervinquière

Plate 88, figs. 1-18, 20-24; pl. 89, figs. 11-12; text-figs. 2a, d, e; 3j, k, l

- 1907 *Flickia simplex* Pervinquière, p. 214, pl. 9, figs. 2a-b, 3a-b, 4, 5a-b; text-figs. 80, 82.  
 1920 *Flickia boesei* Adkins, p. 85, pl. 1, figs. 1-3; text-fig. 9.  
 1925 *Flickia simplex* Pervinquière; Diener, p. 229.  
 1928 *Flickia boesei* Adkins; Adkins, p. 127, p. 121, figs. 5-6.  
 1929 *Flickia simplex* Pervinquière; Collignon, p. 24, pl. 2, fig. 14, 14a.  
 1929 *Flickia pervinquieri* Collignon, p. 4, pl. 2, fig. 15, 15a; text-fig. 14.  
 1931 *Flickia pervinquieri* Collignon; Collignon, p. 76, pl. 3, fig. 21, 21a.  
 1938 *Flickia simplex* Pervinquière; Roman, p. 509, figs. 51, 479.  
 1964 *Flickia simplex* Pervinquière; Collignon, p. 23, pl. 322, fig. 1425.  
 1964 *Flickia pervinquieri* Collignon, p. 23, pl. 322, fig. 1426.

*Types.* Pervinquière specifically cites the original of his pl. 9, figs. 4–5 as 'type' of this species (1907, explanation of pl. 9). Collignon (1929) included this specimen in the synonymy of his *F. pervinquieri*, see below. The specimen, from between Zrissa and bou el Hanèche, Tunisia (Flick Coll.) is preserved in the collections of the Sorbonne, as are the following paratypes; three from Si Abd el Kerim (including the original of Pervinquière's pl. 9, fig. 2a–b), two from Bou tis Bargou (= Pervinquière pl. 9, fig. 3a–b), one from Thala, and two from Guem er Rhezal.

*Other material studied.* Collignon's (1929) material from the Lower Cenomanian of Diego Suarez, Madagascar, in the Collection of the Muséum d'Histoire Naturelle, Paris. The original of Collignon 1964, pl. 322, fig. 1425 from the Lower Cenomanian of Collignon's locality 478, Beraketa sur Sakondry (Manera), Madagascar. The holotype of *F. boesei* Adkins, from the Paw Paw Formation, 400 m east of the Riovista–Waco road and 1.6 km south of Riovista, Texas (Texas Memorial Museum Collections, Austin, no. UT 2140).

The lectotype of *F. pervinquieri*, designated by Kennedy and Klinger 1978, p. 215 is the original of Collignon 1929, pl. 2, fig. 15, 15a, from the Lower Cenomanian east of Antsirane, Madagascar. A second unfigured paratype is from the same horizon and locality, both specimens being housed in the collections of the Muséum d'Histoire Naturelle, Paris. The original of Collignon 1931, p. 36, pl. 3, figs. 21, 22, from the Champs de Tir, Diego Suarez, Madagascar, Besairie Collection, also in the Muséum d'Histoire Naturelle.

The original of Collignon 1964, p. 23, pl. 322, fig. 1426 and over a hundred additional specimens from Beraketa sur Sakondry (Manera), Madagascar, Collignon's Locality 478.

#### Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	11.5(100)	3.5(30)	5.0(43)	0.7	3.1(27)
Paratype 1	5.0(100)	2.5(50)	2.2(44)	1.13	1.2(24)
Paratype 2	7.0(100)	2.8(40)	3.0(43)	0.93	2.0(28)
M. Collignon, 1426	13.3(100)	3.4(26)	4.1(31)	0.83	4.5(34)
M. Collignon A	12.3(100)	3.5(28)	4.3(35)	0.81	4.3(35)
M. Collignon B	12.0(100)	3.4(28)	4.4(37)	0.77	4.0(33)
M. Collignon C	13.1(100)	3.5(27)	4.9(37)	0.72	4.1(31)
M. Collignon D	12.1(100)	3.2(26)	3.9(32)	0.82	4.1(34)
M. Collignon E	12.1(100)	3.2(26)	3.9(32)	0.82	4.0(33)

*Description.* Juveniles are relatively involute, with a small deep umbilicus. The umbilical wall is high and rounded, and the whorl section depressed (whorl breadth to height ratio is up to 1.13). At maturity, coiling is moderately evolute, just over 40% of the previous whorl being covered. The umbilicus comprises 27–35% of the over-all diameter, and is shallow, with a low rounded, outwards sloping wall and an abruptly rounded shoulder. The whorl section is compressed, typically varying between 0.77 and 0.83, with parallel flanks and shoulders which converge to a rounded or fastigate venter with or without a distinct angle over the siphon.

The shell is either smooth, or bears occasional rather irregular prorsiradiate constrictions, conspicuous at the umbilical shoulder, but usually declining across the flank, or rarely developed across the venter where they may be associated with broad folds.

Suture line with broad, low, entire lobes and saddles.

*Discussion.* The type series of *F. simplex* show the change from depressed, inflated juveniles to compressed adults; the holotype is an individual with a particularly well-marked angular venter; others have a much more rounded, broader venter at the same diameter. *F. boesei* Adkins (1920, p. 217, pl. 21, figs. 5–6) was separated from *F. simplex* on the basis of a somewhat broader whorl section and minor suture differences, well within the range of variation of the material before us. Collignon (1929) erected *F. pervinquieri* for specimens with 'an extremely distinct sharp keel'. He included in his synonymy the type of *F. simplex*, but in his description he appears to distinguish his Madagascar specimens from Pervinquière's, although his meaning is not absolutely clear. In any case, in spite of Collignon's statement, his specimens do

not have a sharp keel but merely a fastigate whorl section with a distinctively angular siphonal line.

The absence of ribs or folds readily separates *F. simplex* from *F. costellata* and *F. quadrata*.

*Flickia quadrata* Collignon

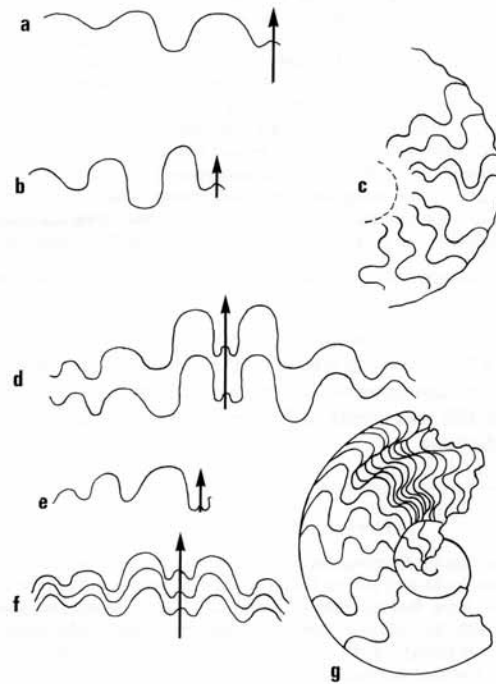
Plate 88, figs. 29-37

1964 *Flickia quadrata* Collignon, p. 23, pl. 322, figs. 1428-1429.

1978 *Flickia quadrata* Collignon; Kennedy and Klinger, p. 212; text-figs. 1-2.

*Holotype*. The specimen from the Lower Cenomanian of Berakata sur Sakondry (Manera), Madagascar figured by Collignon 1964, pl. 322, fig. 1428.

*Other specimens studied*. One paratype, the original of Collignon 1964, pl. 322, fig. 1428, and two other specimens from the Lower Cenomanian of the Collines des Vohipaly (niveau inférieur, Sakaraha),



TEXT-FIG. 2. *a, d, e, Flickia simplex* sutures: *a*, from the original of Collignon 1964, pl. 322, fig. 1425; *d*, the holotype; *e*, the holotype of *F. boesei*. *b, c, F. costellata* sutures: *b*, the paratype; *c*, the holotype. *f, g, Adkinsia bosquensis* sutures: *f* is from BMNH C53887; *g* from BMNH C53896. All figures are  $\times 3$ .

Collignon's locality 485. BMNH C79841 and C79976, from the Lower Cenomanian Mzinene Formation, Locality 181 of Kennedy and Klinger (1975, p. 304), hill slopes east of the road, 1 km. south-east of the store at Ndumu, Zululand, 26° 55' 51" S., 32° 18' 29" E.

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	14.7(100)	3.8(26)	5.5(37)	0.69	—(—)
Paratype	12.6(100)	4.0(31)	4.9(38)	0.81	3.6(29)
BMNH C79976	23.8(100)	8.2(34)	7.5(32)	1.09	7.8(33)
	18.7(100)	6.7(36)	6.3(34)	1.09	6.5(35)

*Description.* The malagassy types are pyritic internal moulds of phragmocones. Coiling is relatively evolute, approximately 37% of the previous whorl being covered in the best preserved specimen. The umbilicus comprises approximately 30% of the diameter, is shallow, with a low, outwards-sloping wall and an abruptly rounded shoulder. The whorl section is compressed (breadth to height ratio is between 0.69 and 0.81) with parallel flanks and a rounded/fastigiolate venter. Early whorls are relatively smooth and may bear a delicate keel, but on the outer part of the last whorl, low broad, prorsiradiate or radial folds and depressions develop on the flanks, strengthening and flexing forwards across the venter to produce a distinct chevron, the venter appearing undulose in profile although retaining angularity over the siphuncle.

The suture line shows a small median element to the external lobe E, a rather narrow lateral lobe L, and a shallow broad U<sub>2</sub>. E/L is larger with a flat top. L/U<sub>2</sub> is smaller and rounded.

The adult specimens from South Africa (Kennedy and Klinger 1978, figs. 1A-K, 2A-B) have mature body chambers at diameters of approximately 24 mm. The umbilicus has widened to 33-35% (as a result of slightly excentric, scaphitoid coiling) and the whorls are slightly depressed, the greatest breadth being a little below mid-flank, the inner flanks being parallel, the outer flanks convergent, and the venter arched and rounded. Ornament consists of rather irregular broad, low, prorsiradiate fold-like ribs, narrow at the umbilical shoulder but widened across the flanks and passing over the venter as a broad, rounded swelling. The interspaces are irregular, some being distinct constrictions. The shell surface is covered by well-developed striae; ribs, constrictions/interspaces, and striae strengthening on the body chamber which has a simple, entire aperture, slightly flared in BMNH C79976 and preceded by a narrow rib in BMNH C79841.

*Occurrence.* *F. quadrata* is known only from the Lower Cenomanian of Madagascar and northern Zululand (South Africa).

*Discussion.* The angular venter and parallel sides of this species suggest affinities with *F. simplex*, some of which develop weak irregular folds. The material referred to that species never, however, develops such a strong ornament as the present species, and within the more than 100 specimens of *F. simplex* studied there is not a demonstrable transition between the two.

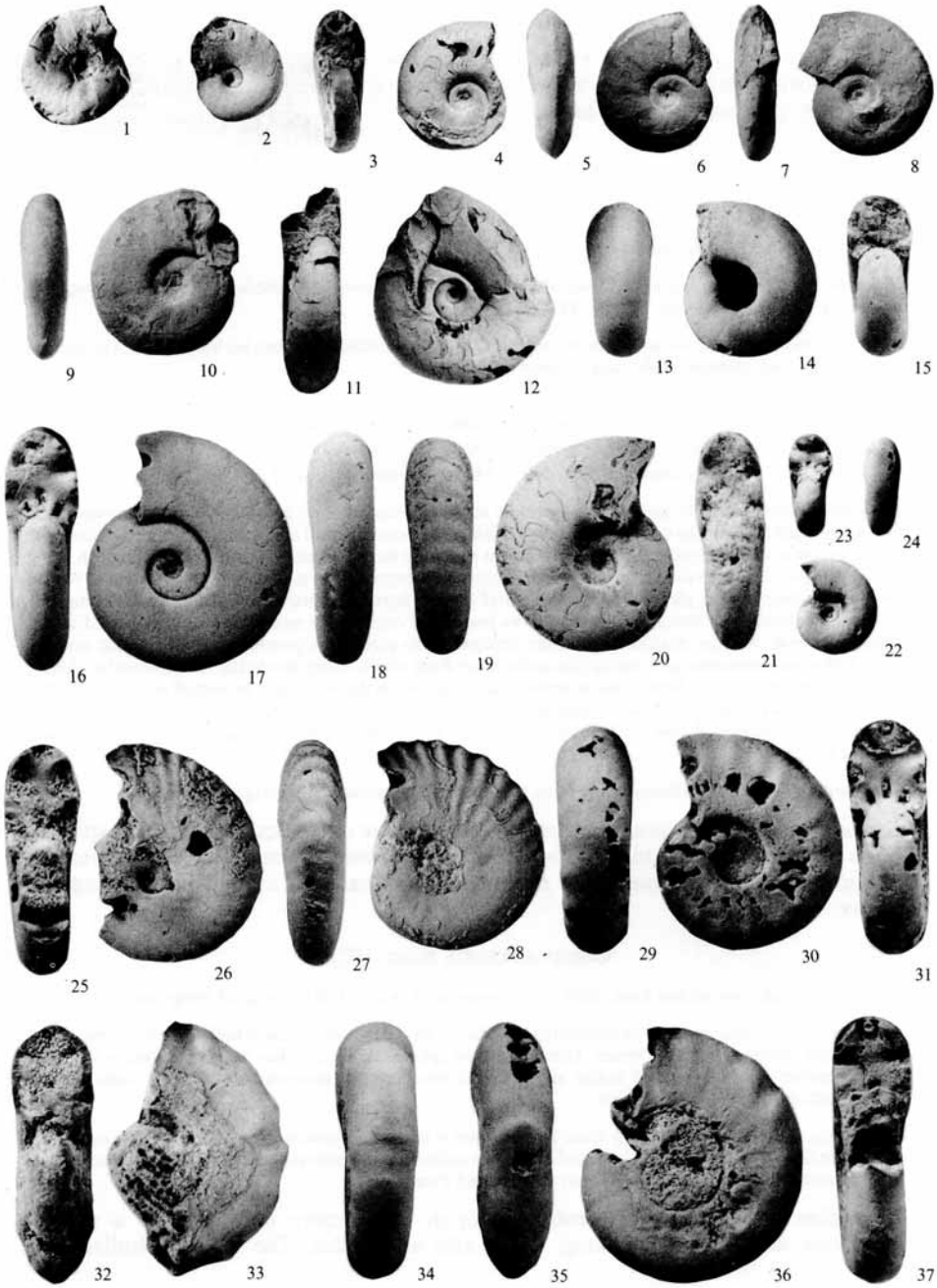
EXPLANATION OF PLATE 88

Figs. 1-18, 21-24. *Flickia simplex* Pervinquière. 1, 2, paratypes, from Guern er Rhezal, Tunisia; 5-8, the holotype, from between Zrissa and Bou el Hanèche, Tunisia; 9-10, a paratype from the same locality; 11-12, 22-24, paratypes from Bou tis Bargon, Tunisia; 13-15, a Malagassy specimen, the original of Collignon's (1946, pl. 322, fig. 1425) *F. simplex*, from the Lower Cenomanian of his Locality 478, Beraketa sur Sakondry (Manera); 16-18, the original of Collignon's (1964, pl. 322, fig. 1526) *F. pervinquierei*, from the same horizon and locality. 20-21, a further Malagassy specimen from this locality, showing the sutures.

Figs. 19, 25-28. *F. costellata* Collignon, 19, 25-26 a paratype and 27-28 the holotype, from the Cenomanian of Beraketa sur Sakondry (Manera), Madagascar.

Figs. 29-37. *F. quadrata* Collignon, 29-31 a paratype, 32-34 a topotype and 35-37 the holotype, from the Cenomanian of Beraketa sur Sakondry (Manera), Madagascar.

All figures are ×2.



WRIGHT and KENNEDY, Ammonite family Flickiidae

*F. costellata* Collignon has a much higher whorl section, a smaller umbilicus, and early whorls with fine, dense, flexuous striae which strengthen into narrow flexuous ribs at the greatest diameters known.

*Flickia costellata* Collignon

Plate 88, figs. 19, 25-28; text-fig. 2b, c

1964 *Flickia costellata* Collignon, p. 23, pl. 322, fig. 1427.

*Holotype.* The specimen from the Lower Cenomanian of Berakata-sur-Sakondry (Manera), Madagascar figured by Collignon 1964, pl. 322, fig. 1427.

*Other specimens studied.* One specimen in General Collignon's Collection, from his locality 485, Collines de Vohipaly, (niveau inférieur, Sakaraha), Lower Cenomanian.

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	12.2(100)	3.5(29)	6.0(49)	0.58	—(—)
Vohipaly spec.	12.3(100)	3.8(31)	6.0(49)	0.63	3.0(24)

*Description.* Both available specimens are wholly septate pyritic internal moulds. Coiling is involute, the umbilicus small (24% of the diameter), shallow, with a low, rounded wall and gently sloping shoulder. The whorl section is very compressed (breadth to height ratios are from 0.58 to 0.63), the greatest breadth being just above the umbilical shoulder, the flanks slightly convergent, with a narrowly archer venter. At the smallest diameter visible, the flanks are ornamented by fine, flexuous prorsiradiate striae, which strengthen across the ventrolateral shoulders and venter as low broad convex ribs and interspaces, projected into a ventral chevron. As size increases, the striae strengthen, to give dense prorsiradiate ribs which arise as striae at the umbilical seam, producing ribs on the lower flank which strengthen to the ventrolateral shoulder, being straight on the inner flank, convex at mid flank, concave on the outer, and projected across the venter, where they are at their greatest development.

Suture with narrow E and L; E/L large, narrow; L/U<sub>2</sub> smaller, broader, and lower with a broad shallow U<sub>2</sub>.

*Occurrence.* *F. costellata* is known only from the Lower Cenomanian of Madagascar.

*Discussion.* This is the most compressed and involute of the described *Flickia* species. In its evolution it resembles *F. simplex* which is, however, smooth. *F. quadrata* has irregular folds, constrictions, and swellings rather than ribs, and also has an angular venter.

Genus ADKINSIA Böse, 1928

*Type species.* *Adkinsia adkinsi* Böse, 1928 = *A. bosquensis* Adkins, 1920 by original designation.

*Diagnosis.* Moderately involute to moderately evolute with a deep umbilicus, elliptical to reniform whorl section with narrowly rounded venter. Ornamented by sparse umbilical bullae which give rise to low ribs. Body chamber shows decline of bullae and crowded low, flexuous prorsiradiate ribs and folds. Suture simple, with entire lobes and saddles.

*Occurrence.* *Adkinsia* is known only from Texas, where it is not uncommon in the Del Rio Clay, occurring in both the *Graysonites lozoi* and *G. adkinsi* Zones. An undescribed species is also known from the succeeding Buda Limestone (*Budaiceras hyatti* Zone) (Young and Powell, 1978).

*Discussion.* *Adkinsia* differs from *Flickia* in being more inflated with a deeper umbilicus, and in having strong, sparse ribs and bullae. The ribs and bullae also

distinguish it from *Ficheuria*, which has a much deeper umbilicus with a high wall and sharply angular umbilical shoulder, and in many cases, minor incisions in lobes and/or saddles.

*Adkinsia bosquensis* Adkins

Plate 89, figs. 1-10, 13-29; text-figs. 2f, g; 3m, n, o

- 1920 *Flickia* (?) *bosquensis* Adkins, p. 87, pl. 1, fig. 4; pl. 4, fig. 11; text-fig. 10.  
 1928 *Adkinsia adkinsi* Böse, p. 237, pl. 8, figs. 9-14.  
 1928 *Adkinsia sparsicosta* Böse, p. 238, pl. 8, figs. 15-20.  
 1928 *Adkinsia tuberculata* Böse, p. 240, pl. 8, figs. 21-26.  
 1928 *Adkinsia bosquensis* Adkins; Böse, p. 242, pl. 9, figs. 1-6.  
 1928 *Adkinsia semiplicata* Böse, p. 246, pl. 9, figs. 7-12.  
 1928 *Adkinsia adkinsi* Böse; Adkins, p. 217.  
 1928 *Adkinsia sparsicosta* Böse; Adkins, p. 217.  
 1928 *Adkinsia tuberculata* Böse; Adkins, p. 218.  
 1928 *Adkinsia bosquensis* (Adkins); Adkins, p. 218, pl. 23, fig. 6.  
 1928 *Adkinsia semiplicata* Böse; Adkins, p. 218.  
 1938 *Adkinsia adkinsi* Böse; Roman, p. 509.  
 1957 *Adkinsia tuberculata* Böse; Wright, p. L409, fig. 527, 3.

*Holotype.* Adkin's original specimen, UT 21411, Del Rio Clay, west bank of the South Bosque River, 150 yards south of the bridge on the Speegleville road, 5.5 miles W. of Waco Courthouse, Texas.

*Dimensions*

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
UT 21583 <i>A. bosquensis</i>	15.2(100)	8.2(54)	5.7(38)	1.43	4.6(30)
UT 21574					
Holotype, <i>A. adkinsi</i>	13.4(100)	—	5.7(43)	—	3.0(22)
Holotype, <i>A. adkinsi</i>	— (—)	4.2(—)	5.0(—)	0.84	— (—)
UT 21581					
Holotype, <i>A. sparsicosta</i>	16.2(100)	7.0(43)	5.9(36)	1.18	5.0(31)
UT 21580					
Holotype, <i>A. tuberculata</i>	15.0(100)	6.7(45)	5.6(37)	1.20	4.7(31)
UT 21582					
Holotype, <i>A. semiplicata</i>	12.0(100)	5.3(44)	5.0(41)	1.1	2.9(24)

*Other specimens studied.* The holotype of *A. adkinsi* Böse, University of Texas Memorial Museum no. 21574, Del Rio Clay, east side of Santa Fe Railroad Track, 4.5 miles south of McGregor, Texas. The holotypes of *A. sparsicosta* Böse, UT 21581, from the same horizon and locality. The figured specimen, referred to by Böse (1928) as *A. bosquensis*, UT 21583, same horizon and locality. The holotype of *A. semiplicata* UT 21582, same horizon and locality. Holotype *A. tuberculata* Böse, UT 21580, from the Del Rio Clay, east bank of South Bosque River, 2 miles south of South Bosque, Texas. Numerous other Paw Paw specimens in the Texas Memorial Museum (Adkins Collection etc.) and U.S. National Museum (Renfro Collection etc.).

BMNH C53875-53900, Del Rio Clay, McGregor, McLennan County Texas.

*Description.* Moderately involute to moderately evolute, with an umbilicus of moderate breadth (21-31%), fairly deep, with a steep rounded wall and abruptly rounded, but not angular umbilical shoulder. Whorl section slightly compressed to depressed (breadth to height ratios vary from 0.84 to 1.43), the greatest breadth at the umbilical bullae, the section with rounded to swollen flanks and a narrowly rounded venter. Early whorls are smooth, or with weak bullae, the outer whorl of the phragmocone bearing 8-12 strong to weak bullae which give rise to single low, broad convex prorsiradiate ribs which decline across the flanks and may or may not extend to the venter. Body chambers are ornamented by low, irregular prorsiradiate flexuous ribs or folds, the bullae tending to decline.

Sutures are simple with entire lobes and saddles, relative proportions varying widely. Septal spacing variable, being both distant and crowded in similar sized individuals, or showing groupings of two to three closely spaced sutures with wider gaps between.

*Occurrence.* Lower Cenomanian, Del Rio Clay of Texas.

*Discussion.* Böse recognized no fewer than five species of *Adkinsia* on the basis of seven specimens, all the species occurring together at one locality. On the basis of the large collections now available, it is clear that a continuum exists between all named forms. The slender variant with a compressed whorl section and weak bullae is *A. adkinsi*; *A. semiplicata* is more inflated with stronger bullae and has low ribs on the flank; *A. bosquensis* of Adkins is stronger ribbed, as is *A. tuberculata*, and the *A. bosquensis* of Böse is the most inflated, strongly bullate form. Every variant exists between these, whilst there is wide variation in sutures depending on shell form, position in relation to rib, bulla or interspace, as shown in the illustrations.

There are no other Flickiidae with which *Adkinsia* is liable to be confused.

#### EVOLUTIONARY RELATIONSHIPS

The difficulties of deciphering the relationships of the Flickiidae are compounded by the problems of correlation at the Albian–Cenomanian boundary. These result from the occurrence of ammonites in two distinctive facies and preservations, correlation of which is not yet fully possible: the pyritic clays with ‘submantellicerine’ nuclei, known from North Africa, Texas, Mexico and Madagascar, and the limestone/sandstone facies of Europe, India, and elsewhere (Kennedy 1971, Kennedy and Hancock 1971, 1977). In particular, we do not know how the former successions relate to the type areas, and whether they pre- or post-date the base of the standard Cenomanian sequence.

The genera under review here can, however, be placed in approximate order: Youngest–Oldest:

5. *Adkinsia (bosquensis)*.
4. *Flickia (simplex, quadrata, costellata)*, commonest in the earliest Cenomanian.  
Rare *Ficheuria (rudelli, pernoni, pusilla)*.

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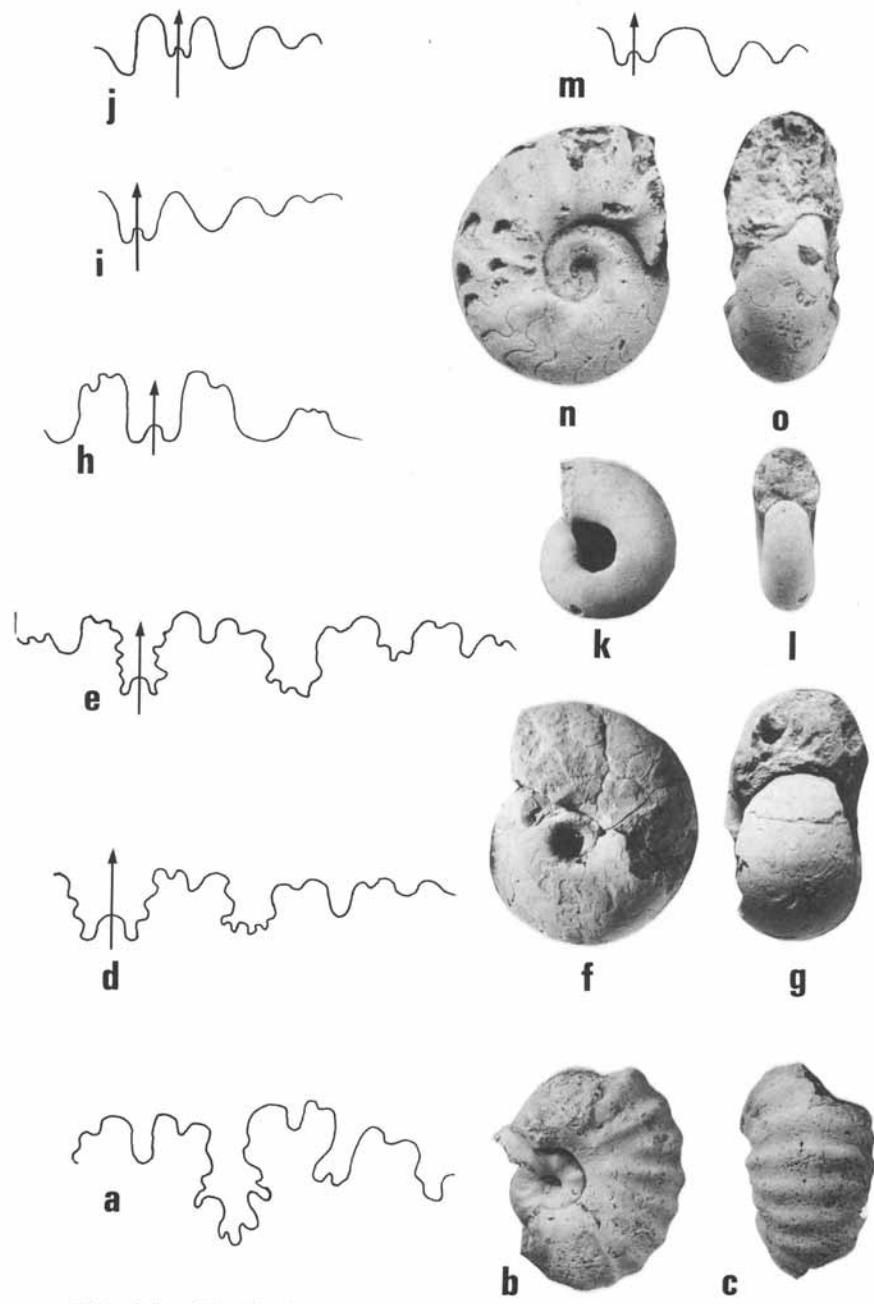
#### EXPLANATION OF PLATE 89

Figs. 1–10, 13–29. *Adkinsia bosquensis* (Adkins). 1–3, the original of Böse (1928) pl. 9, figs. 1–6, UT 21583; 4–6, the holotype of *A. tuberculata* Böse, UT 21580; 7–8, the holotype of *A. bosquensis*, UT 21411; 9–10, WSA 2674, a strongly ribbed example; 13–14, BMNH C53888; 15–18 the holotype of *A. adkinsi* Böse, UT 21574; 17–19 the holotype of *A. semiplicata* Böse, UT 21582; 20–22, BMNH C53896, showing the inner whorls and variable sutural spacing; 23–25 the holotype of *A. sparcicosta* Böse, UT 21581; 26–27, BMNH C53887, showing cyclic grouping of septa and 28–29, BMNH C93886, a mature adult retaining body chamber. All specimens are from the Cenomanian Del Rio Clay of Texas; see text for precise localities.

Figs. 11–12. *Flickia simplex* Pervinquierè, the holotype of *F. boesei* Adkins, UT 2140, from the Paw Paw Formation, Albian, 400 m east of the Riovista–Waco road and 1.6 km south of Riovista, Texas.

All figures are  $\times 2$ .





TEXT-FIG. 3. Evolution of the Flickiidae. a-c, adult *Salaziceras salazacense* and suture; d, juvenile suture. e-g, adult *Ficheuria kiliani* and suture. h, mature suture of *F. pernoni*, i, mature suture of *F. pusilla*. j, mature suture and k, l, inflated juvenile whorls of *Flickia simplex*. m, n, o, adult *Adkinsia bosquensis* and suture.



WRIGHT and KENNEDY, Ammonite family Flickiidae

3. *Ficheuria* (aff. *peroni*); rare *Flickia* (*simplex*) in the latest Albian.
2. *Ficheuria kiliani*—late Albian.
1. *Salaziceras salazacense*—late Albian.

We would suggest (text-fig. 3) that *F. kiliani*, with the most complex sutures seen in the genus, is derived from *Salaziceras* by paedomorphosis, the mechanism by which several other Cretaceous micromorphs with simplified sutures arose (*Falliceras*—Kennedy and Cooper 1977; *Protacanthoceras*—Wright and Kennedy, in press). *Ficheuria* and *Salaziceras* have a similar whorl section and deep umbilicus, while juvenile *Salaziceras* are feebly ribbed and have sutures very close to those of adult *F. kiliani*. The transition thus involved the development to maturity of juvenile *Salaziceras* features, accompanied by the reduction of ribbing to mere folds on the body chamber and a sharpening of the umbilical shoulder.

From *F. kiliani*, there is evidence for progressive sutural simplification (text-fig. 3), *F. kiliani*→*F. rudelli*→*F. pusilla*, together with the loss of all but the weakest ornament on the phragmocone, although even *F. pusilla* with the simplest of sutures, retains folds and ribs on the body chamber.

*Adkinsia* apparently arose in the southern United States as a short-lived endemic offshoot of *Ficheuria* with entire lobes and saddles. The genus retains the inflated form of its ancestor, but the umbilical shoulder rounds, the venter becomes higher and narrower, and sparse bullae and ribs develop. Body chambers retain, however, the irregular ribs and folds of mature *Ficheuria*.

*Flickia* seems also to be a direct offshoot of *Ficheuria* with entire lobes and saddles. The apparently earliest species, *F. simplex*, is the most inflated of the genus, with the deepest umbilicus, and, when juvenile, a *Ficheuria*-like form but with a rounded umbilical shoulder. From this arose the compressed and flat-sided, ribbed *F. costellata*, and the weakly fastigate *F. quadrata* with the reappearance of the basic ribs, folds, and constrictions of the ancestral *Ficheuria*.

The Flickiidae were short-lived, being limited to the latest Albian and Cenomanian, but their evolution demonstrates two relatively uncommon traits in ammonite evolution: size reduction and sutural simplification to the extent that these Cretaceous dwarfs returned to the form of the ammonoid archetype.

*Acknowledgements.* We thank General M. Collignon (Moirans, Isère), Dr. J. Sornay (Paris), Dr. D. Pajaud (Paris), Professor T. Matsumoto (Kyushu), Mr. C. Duerden and Professor K. Young (Austin), Dr. M. K. Howarth, Mr. D. Phillips, and Dr. J. M. Hancock (London), and Dr. M. R. Cooper (Oxford) for their assistance in several respects.

Financial assistance from the NERC and from Wolfson College, Oxford, is gratefully acknowledged by Kennedy. The help of the staff of the Geological Collections, University Museum, Oxford, is also gratefully appreciated.

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Typescript received 9 July 1978

Revised typescript received 6 November 1978