BIVALVIA OF THE SPILSBY SANDSTONE AND SANDRINGHAM SANDS (LATE JURASSIC-EARLY CRETACEOUS) OF EASTERN ENGLAND

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SIMON R. A. KELLY

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ABSTRACT

In part 2, the systematic description continues of the bivalves of Middle Volgian to Ryazanian age of the marine Spilsby Basin. This section includes descriptions of forms from the orders Trigonoida and Veneroida, including the families Trigoniidae (concluding part)) Lucinidae and Astartidae. 13 taxa from 7 genera are described, of which one subgenus, *Pinguiastarte* subgen. nov., and 4 species are new: *Discoloripes septentrionalis, Mesomiltha biscathorpensis, Lyapinella rawsoni, Pressastarte (Pinguiastarte) lincolnshirensis.*

Bivalves des Spilsby Sandstone et Sandringham Sands (Jurassique terminal-Crétacé basal) de l'est de l'Angleterre. 2ième partie.

RÉSUMÉ

Dans la deuxième partie, la description continue des Bivalves d'âge Volgien Moyen a Ryazanien du Bassin marin de Spilsby. Cette partie comprend la description des formes appartenant aux ordres Trigonioida et Veneroida, comprennant les familles Trigoniidae (partie dernier), Lucinidae et Astartidae. 13 taxa repartis dans 7 genres sont décrit comprenant Pinguiastarte sousgen. nov.; 4 espèces sont nouveaux, comprenant: Discoloripes septentrionalis, Mesomiltha biscathorpensis, Lyapinella rawsoni, et Pressastarte (Pinguiastarte) lincolnshirensis.

Bivalvia des Spilsby-Sandsteins und der Sandringham-Sande (spät-Jura bis früh-Kriede) von Ost-England. Teil 2.

ZUSAMMENFASSUNG

In Teil 2 werden die Bivalven des mittleren Wolgium bis Ryazan aus dem marinen Spilsby-Becken beschrieben. Er enha Beschreibungen der Vertreter den Ordnungen Trigonoida und Veneroida, und zwar der Familien Trigoniidae (abschliessender Teil), Lucinidae und Astartidae. 13 Taxa aus 7 Gattungen werden beschrieben, einschliesslich Pinguiastarte untergattung nov.; 4 Arten sind neu: Discoloripes septentrionalis, Mesomiltha biscathorpensis, Lyapinella rawsoni, und Pressastarte (Pinguiastarte) lincolnshirensis.

PESIOME

Во второй части продолжено систематическое описание средневолжских-рязанских пеленинод морского бассейна Спилсби. Эта часть содержит описание таксомов из отрядов Trigonoida и Veneroida, иключая семейства Trigoniidae (заключительная часть), Lucinidae и Astartidae. Описаны 13 таксовов, принадлежащих 7 родам, из которых один подрод, Pinguiastarie, и 4 вида — новые: Discoloripes septentrionalis, Mesomitha biscathorpensis, Lyapinella rawsoni, Pressastarie (Pinguiastarie) lincolnshirensis.

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LAEVITRIGONIA

anterior margin where some are fused together to form approximately commarginal ribs. The Whitchurch Sands specimen is probably Ryazanian, hence the Spilsby Sandstone specimen may also be of this age. *L. manseli* is well known from the Middle Volgian, Portland Stone, of southern central England. The Spilsby specimen is the northernmost example of *Laevitrigonia* in the Upper Jurassic to Lower Cretaceous of northwest Europe. As it has been reworked into the Boulder Clay, which in this region radiates southwards from the Wash (Kelly *in* Kelly & Rawson, 1983), it is likely to have originated from further north within the Spilsby Basin.

Kelly (1988) described L. (L.) cineris from the Cinder Beds Member at the base of the Durlston Formation in Dorset. This differs from L. (L.) manseli in the lack of vertical and oblique rows of tubercles and having only low sub-commarginal ornament on the flank.

In 1984 and 1987 the author had further opportunity to examine Laevitrigonia from the Russian Platform in Moscow. Kelly (1984a, p. 94) stated that the age of L. (L.) koprinensis Gerasimov was Ryazanian. However, this remark is erroneous and the age is actually Volgian. Nevertheless, undescribed material in the Museum of A. P. and M. V. Pavlow, Moscow University (P. A. Gerasimov collection), from the Ryazanian of the Leshchinski Ravine, of Mikhaylov, Ryazan Oblast, indicates that the subgenus is definitely present on the Russian Platform in Lower Cretaceous time.

Distribution. Middle Volgian to Ryazanian of central and southern England; ?Middle Volgian or Ryazanian of eastern England.

Laevitrigonia (Laevitrigonia) wightensis (Strand, 1928) Pl. 16, fig. 2

- v. 1875 Trigonia Michelotti de Loriol var.; Lycett, p. 92, pl. 20, fig. 7 ['Portland Limestone', Wiltshire; BMNH, Cunnington Collection].
- v. 1883 Trigonia gibbosa J. Sowerby; Keeping, p. 156 [Derived, base of Lower Greensand, Potton, Bedfordshire].
- v.* 1928 Trigonia wightensis sp. nov. Strand, p. 71 [Type designation].
- v. 1929a Trigonia wightensis Strand; Cox, p. 160, pl. 3, fig. 1 [Portland Stone, southern England; BGS 48594].
- . 1964 Laevitrigonia wightensis (Strand); Casey & Bristow, p. 123 [Whitchurch Sands, central England].
- v. 1983b Laevitrigonia wightensis (Strand); Kelly, p. 290 [Reworked into Lower Greensand, Potton, Bedfordshire].

Type specimen. Holotype by monotypy; BMNH Cunnington Collection, 88928; originally figured by Lycett, 1875, pl. 20, fig. 7; Portland Stone, Greenlands Farm, near Devizes, Wiltshire. Casey & Bristow (1964) have interpreted the holotype as coming from the Whitchurch Sands as opposed to the Portland Beds. Thus its age may be as late as Lower Ryazanian.

Material. A single specimen, SMC B.85668, labelled 'Lower Greensand, Potton, Bedfordshire' preserved as replaced calcite shell with some buff shelly calcareous matrix infilling the umbo. It is believed here that the specimen represents part of the reworked fauna occurring in the base of the Lower Greensand. Its precise original stratigraphic horizon is not certain, but it could be from the top of the Portland Stone and therefore be of Middle Volgian age.

Description. The single value is incomplete in the ventral region. It is of medium size, with length in excess of 37 mm and height in excess of 26 mm; suboval in outline, with low umbo and small, incurved, weakly opisthogyrate beak located just to anterior of mid-line; anterior region prominent; posterodorsal margin convex; juvenile flank ornament of commarginal ribs only; in later growth tubercles develop first on the posterior of flank ribs and later form on whole flank; wide, smooth, antecarinal region; posterior carina angular in juvenile, later becoming more rounded, bearing low, poorly developed tubercles; posterior area smooth and flat, with mid-area groove ornamented by growth lines (juvenile part obscured) and divided by mid-area groove; escutcheon carina weak and lacking tubercles; escutcheon smooth and concave.

Remarks. L. wightensis is distinguished from *L. manseli* by its commarginal, as opposed to oblique, flank ornament. *L. damoniana* (de Loriol, 1867) has a much more regular ornament over the flank, and the antecarinal region is less prominent. Well preserved specimens of *L. damoniana* occur in the upper parts of the Portland Stone in Wiltshire and Dorset.

L. (L.) cineris Kelly, 1988 differs from L. (L.) wightensis by the absence of strong tuberculation and by having only low sub-commarginal ornament on the flank.

Occurrence. Portland Stone, Middle Volgian, of central and southern England; age uncertain in Spilsby Basin.

Subclass HETEROCONCHIA Hertwig, 1895

Remarks. The broad classification of Pojeta (1971, p. 26) is followed here. The Heteroconchia embraces the subclass Palaeoheterodonta, comprising the orders Trigonoida and Unionoida (ommitted in Kelly 1984a, p. 81) and the Heterodonta (Neumayr, 1884) as used by Moore (ed. 1969) and Boss (1982).

Although Bernard-type (1895) tooth designations are used in the following text, the homologies suggested by this tooth numbering system do not necessarily exist (Morris 1978). However, within superfamilies, such homologies are likely to be close to reality. Bernard's system of notation for hinge teeth is followed here as it is particularly useful for description and comparison of hinge lines, which are otherwise difficult to discuss verbally using the more objective Steinmann-type notation as used *e.g.* by Boyd & Newell (1969).

In Bernard's system, as used herein, Arabic numerals = cardinal teeth, with suffixes a & b (indicating anterior and posterior respectively), A = anterior lateral teeth, P = posterior lateral teeth, Roman numerals = lateral teeth, O = sockets, brackets () denote weak development of the teeth or sockets and n = nymphs.

The orientations of dimensions used in measurements of heteroconchs and anomalodesmatid bivalves are given in Text-fig. 60.



TEXT-FIG. 60. Orientation of dimensions measured of heteroconch and anomalodesmatid bivalves. B = breadth (with valves in occlusion), B' = breadth (single valve), H = total height, Hh = height up to top of hinge, L = total length, La = length of anterior, Le = length of escutcheon, Lli = Length of ligament, Llu = length of lunule, LV = left valve, RV = right valve.

Order VENEROIDA Adams & Adams, 1856 Superfamily LUCINOIDEA Fleming, 1828 (ex Lucinidae Fleming, 1828) Family LUCINIDAE Fleming, 1828

Remarks. Despite the considerable works of Chavan (1937–1938; *in* Moore (ed.), 1969) the relationships between the subfamilies of the Lucinidae are not well understood, and especially those of the Mesozoic members. Bretsky (1976) preferred not to use suprageneric classification in her study which was based largely upon post-Mesozoic lucinids. Because of the uncertainty of the relationships between Mesozoic lucinids, it is preferred here to follow Bretsky and not use subfamilies. Bretsky's remark that Mesozoic lucinids are only common in few localities is an understatement. In the present author's experience, they are common at many localities in the marine Mesozoic of Europe.

Genus CODAKIA Scopoli, 1777

Type species. By monotypy; Chama codak Adanson, 1757 (fide Bretsky 1976) (errore pro C. codok, pre-Linnean, invalid; = Venus orbicularis Linné, 1758).

Diagnosis. Medium sized lucinid with concentric or reticulate sculpture; lunule rather large, asymmetrical; ligamentary groove of moderate extent; posterior lateral teeth small.

Remarks. Chavan (*in* Moore (ed.) 1969, p. N494) subdivided *Codakia* into two subgenera. *C.* (*Codakia*) is distinguished by reticulate ornament and a small lunule, with obsolete posterior lateral teeth. It ranges from Palaeocene to Recent. *C.* (*Epilucina*) Dall, 1901, with type species by original designation, *Lucina californica* Conrad, 1837, Recent, western U.S.A., is smaller with concentric ornament only; the lunule is large and posterior lateral teeth are small. It ranges from Upper Jurassic to Recent. The range in morphology of *C. crassa*, described below covers both these subgenera, and so subgeneric level is unassigned. Although Chavan recognized *C. (Epilucina*) from the Jurassic, Bretsky (1976) only recognized it in the Pliocene to Recent.

Codakia crassa (J. de C. Sowerby, 1827) Pl. 21, figs 1-8; Text-fig. 61

- *.p 1827 Lucina crassa sp. nov. J. de C. Sowerby, p. 108, pl. 557, fig. 3. [probably Volgian, Spilsby Sandstone, Lincolnshire only; non Oxfordian, Sutherland, Scotland].
- ?non 1828 Lucina crassa Sowerby; Fleming, p. 443 [Oolite].
- non 1843 Lucina crassa J. de C. Sowerby; Morris, p. 89 [Calcareous Grit, Braambury, Brora, Sutherland, Scotland].
- non 1849 Lucina crassa Sowerby; Brown, p. 215, pl. 89, figs 9,10 [Calcareous Grit, Cloughton Wyke, North Yorkshire].
- non 1853 Lucina crassa Sowerby var.; Morris & Lycett, p. 68, pl. 6, fig. 13 [= Lucina anglica (Rollier, 1913, p. 159), Great Oolite, Bathonian, Minchinhampton, Gloucester].
- non 1854 Lucina crassa J. de C. Sowerby; Morris, p. 207 [Calcareous Grit, Braambury, Brora, Sutherland, Scotland].
- 1867 Lucina crassa J. de C. Sowerby; Judd, p. 251 [Spilsby Sandstone, Lincolnshire].
- non 1889 Lucina Crassa; Brown, p. 108, pl. 89, figs 9, 10 [horizon not stated; see Brown 1849, above].
- 1895 Lucina crassa Sowerby; Woodward, p. 377 [Spilsby Sandstone, Lincolnshire].
- v 1906 Lucina sp.; Woods, p. 152, pl. 24, figs. 2,3 [Spilsby Sandstone, Donington and Holton, Lincolnshire]
- 1948 Lucina crassa J. de C. Sowerby; Cox & Arkell, p. 33 [Sowerby's Sutherland type material discussed].

Type specimens. Sowerby (1827) recorded syntypes: 'Found by Mr. Weir in Sandstone at Horncastle', Lincolnshire, of which a specimen was figured, 'and by R. I. Murchison, Esq. at Brambury Hill, Sutherland', which was unfigured. None of these specimens have been traced. A neotype is designated here: BGS Zu819/822, Lower Spilsby Sandstone, *preplicomphalus* Biozone, Upper Volgian, locality 10, West Keal, Lincolnshire. The species, as interpreted here, is only known from Middle and Upper Volgian specimens from eastern England; examples from the Oxfordian of Sutherland are excluded.

Material. 14 specimens: including BGS CE3453, Zu259, Zu268, Zu270-271, Zu370, from erratic boulders of Lower Spilsby Sandstone, oppressus Biozone, Middle Volgian, locality 12, Leziate, Norfolk; Zu724, Lower Spilsby Sandstone, preplicomphalus Biozone, Upper Volgian, locality 10, West Keal, Lincolnshire; BMNH L.60005, Spilsby Sandstone, horizon unknown, Holton, Lincolnshire; SMC B.11366, Spilsby Sandstone, horizon unknown, Donington, Lincolnshire.

Diagnosis. Adult shell normally 20–25 mm in length, commissural outline subcircular; exterior almost smooth with delicate commarginal growth lines and sometimes fine radial grooves.

Description. Adult shell of medium size, robust, with length usually 20–25 mm; commissural outline subcircular with low umbo and small sharp prosogyrate beak; lunule obscure but appears narrow and shallow in right valve and deeper in left; flank almost smooth but ornamented by delicate growth lines; in some specimens (Zu271, Pl. 21, fig. 6) fine radial grooves are present; undifferentiated posterior area; internally, hinge line well developed (Text-fig. 61), with formula:



TEXT-FIG. 61. Internal morphology of *Codakia crassa* (J. de C. Sowerby), showing hinge scale bar gave teeth numbered according to Bernard (1895), pallial line and muscle scars. Left and right valve based on BGS CE3453.

Left valve: AII short and bluntly laminar; AIV short and feeble; short deep socket for AIII; all anterior teeth situated directly under anterior end of lunule; 2 is narrow, laminar and opisthocline with weak socket in front and well developed triangular socket behind; 4b laminar and opisthocline and close to ventral margin of nymph which bears deeply set ligament groove; posterior end of hinge thickened but with weak traces of short PII with socket above for PIII; right valve: AIII is bluntly laminar and with ill-defined socket above; 3a small and laminar, running near vertically below umbo, but with dorsal end obscured by lunule; large triangular socket for 2; 3b prominent, weakly opisthocline, narrowly tapered but triangular in posterior aspect; large triangular socket for 4b bordering elevated nymph; posterior end of hinge thickened, but bearing minute PIII; shell interior smooth or pustulose; margin smooth and thickened below pallial line; ovate posterior adductor scar; anterior adductor scar elongate, close to pallial line and only weakly impressed; some specimens show weak oblique median groove.

Measurements. (In mm, see Text-fig. 60)

	Valve	L	Н	В
BGS CE3453	L&R	21	22	8
Zu259	R	20	21	6'
Zu268/70	L	24	25	5'
Zu271	R	23	23	6'
Zu369/70	L	21	22	5'
Zu724	L	22	23	5'
Neotype: Zu819/22	L	25	25	6'
BMNH L.60005	R	25	25	5'

Remarks. Sowerby's (1827) original description was brief: 'Nearly orbicular, convex; covered with thick slightly elevated, concentric laminae; superior margin obtuse; lunule linear, concealed; valves thick. A little wider than long, rather flat in the middle, and irregular; the beaks are very small'. His figured specimen is extremely close in profile to that of Zu268 (Pl. 21, figs 5a, b) and the commarginal ornament identical, but lacks the fine radial grooves. There is some doubt that the figured type came from an erratic block and that it was of Cretaceous age as suggested by Cox and Arkell (1948, p. 33). Judd (1867) stated that Sowerby's specimen came from the 'sandstone at Bolingbroke' from which Spilsby Sandstone lucinids are known *in situ*. All dateable specimens collected so far have been of Middle to Upper Volgian age.

The specimen from Holton which was described by Woods (1907, pl. 23, fig. 3) is much more circular in commissural outline than the internal mould from Donington which he figured (1907, pl. 23, fig. 2). The difference is probably due to the contrasting preservations.

Varieties of C. crassa are recorded (see Cox & Arkell 1948; Stoll 1934), but these appear unrelated to the Spilsby and Sandringham specimens.

Mesozoic lucinids with radial ornament are rare, and it is principally for this reason that *Lucina crassa* is placed in *Codakia*. Contejean (1860) described *L. radiata* from the Kimmeridgian of Montbeliard, France; this large species shows similar radial ornament to *C. crassa*, but its umbo is broader and more projecting and the hinge is unknown.

Occurrence. Middle and Upper Volgian of eastern England.

Genus **DISCOLORIPES** Wellnhofer, 1964

Type species. By original designation Loripes (Discoloripes) gerasimovi Wellnhofer, 1964, p. 81; Neuburger Bankkalke, Lower Volgian, Unterhausen, Bavaria, Germany.

Diagnosis. (Emended) Subovate to subquadrate; exterior ornament of raised, slightly irregular, commarginal lamellae; posterior area weakly demarcated; hinge with four cardinals, 3a usually weak, 3b sometimes bifid, 2 and 4b; moderately developed AIII clear of lunule but AIV may be obscured by lunule; posterior laterals feeble or not developed; dental formula:

RV	AIII	0	3a	0	3b	0	n	(0)
\mathbf{LV}	0	(AIV)	0	2	0	4b	n	(PII)

anterior adductor scar elongate, recurved and slightly divergent from pallial line.

Remarks. Wellnhofer's (1964) tooth numbering is modified in the above scheme to be compatible with other lucinids described here. He did not recognize interior pustules within the type species, but other specimens that he referred to (*e.g.* Gerasimov 1955, pl. 6, fig. 10) show these. Duff (1978, p. 91) regarded such pustules as being restricted to some members of the Myrteinae and Milthinae.

Discoloripes was originally placed by Wellnhofer (1964) as a subgenus of Loripes, but it is felt safer here to raise it to full generic level and thus isolate it from Loripes sensu stricto as that genus does not appear until the Oligocene (Chavan in Moore (ed.) 1969). The relationship between these two genera is speculative at present.

Discoloripes fischerianus (d'Orbigny, 1845b) Pl. 21, fig. 17; Pl. 22, figs 1–21; Text-fig. 62

- 1837 Astarte elegans Sowerby; Fischer de Waldheim, p. 175, pl. 46, figs 6-7 [Yausa, Moscow; non J. Sowerby, 1816, p. 86, pl. 137, fig. 3].
- 1840 Lucina lyrata Phillips; Buch, p. 98, pl. 3, figs 1, 2 [Jurassic, Orenburg, central Russian Platform; non Phillips 1829].
- 1843 Astarte elegans Sowerby; Fischer de Waldheim, p. 127, pl. 5, fig. 2 [Khoroshevo, central Russian Platform; non J. Sowerby].
- *. 1845b Lucina Fischeriana sp. nov. d'Orbigny, p. 458, pl. 38, figs 31-32 ['Oxfordien'; Saragula, central Russian Platform].
- 1846 Unlabelled figure; Rouillier, pl. E, figs a & b only [non figs c & d; fide Gerasimov 1955, p. 66].
- p 1848 Lucina lyrata Phillips var. pinguis nov. Rouillier, p. 276, figs 6A, B ['seconde étage', Moscow; non figs 6C, D, fide Gerasimov (1955, p. 66)].
 - 1850a Lucina Fischeriana d'Orbigny; d'Orbigny, p. 366 ['Oxfordien', Saragula; central Russian Platform].
 - 1861c Lucina Fischeriana d'Orbigny; Trautschold, p. 419 [Moscow; compared to L. lyrata].
- 1862 Lucina Fischeriana d'Orbigny; Trautschold, pp. 371, 386 [Jurassic, Moscow, central Russian Platform].
- 1868 Lucina Fischeriana d'Orbigny; Eichwald, p. 653 ['Néocomien', near Orenburg and Khoroshevo, central Russian Platform].
- 1931 Lucina Fischeri d'Orbigny; Sokolov & Bodylevsky, p. 74 [Janusfjellet Formation, Volgian, Spitsbergen].
- 1933 Lucina fischeri d'Orbigny; Weir, p. 694, pl., fig. 19 [Janusfjellet Formation, Volgian, Spitsbergen].
- v? 1936 Lucina sp. nov. aff. L. inaequalis d'Orbigny; Spath, p. 123, pl. 46, figs 1a, b only [Middle Volgian, Milne Land, East Greenland; non pl. 50, fig. 8 = D. septentrionalis sp. nov., see below].
- pv. 1955 Loripes fischerianus (d'Orbigny); Gerasimov, p. 66, pl. 6, 4-9 only [Middle Volgian, Moscow, central Russian Platform; non fig. 10 = D. septentrionalis sp. nov., see below].
 - ? 1958 Lucina (?) sp.; Bodylevsky in Bodylevsky & Shulgina, p. 20, pl. 3, fig. 2 [Middle Volgian, borehole, Lower Yenissei River, Siberia].

- ? 1967 Cyprina (?) sp. (aff. Loripes fischerianus d'Orbigny); Pchelina, p. 143 [Janusfjellet Formation, Volgian, Spitsbergen].
- pv. 1969 *Loripes fischerianus* (d'Orbigny); Gerasimov, p. 76, pl. 6, fig. 6 [Middle Volgian, Moscow, central Russian Platform].
 - ? 1977 Cyprina (?) sp. (aff. Loripes fischerianus d'Orbigny); Pchelina, p. 188 [Janusfjellet Formation, Lower Volgian, Spitsbergen].

Type specimens. Syntypes (d'Orbigny 1845b) were collected by Verneuil and Keyserling from glauconitised concretions at Saragula, near Orenburg. Untraced; not present in Museum d'Histoire Naturelle, Paris (J. Cl. Fischer, pers. comm. 1991) or in the Ecole des Mines Collection, Lyon (J. Prieur, pers. comm. 1991).

Material. 50 specimens: including BGS Zu3422-3, Zu3538, Lower Spilsby Sandstone, primitivus Biozone, Upper Volgian, locality 3, Nettleton and Zu694-5, Zu703/4, Zu710-15, Zu730, Zu 817/8, Zu887, Zu4031/2 Lower Spilsby Sandstone, preplicomphalus Biozone, Upper Volgian, locality 10, West Keal, Lincolnshire; BMNH L.92484, Spilsby Sandstone, north of Spilsby, Lincolnshire. Abundant but poorly preserved internal moulds occur in the Basal Spilsby Nodule Bed at locality 3 (e.g. Zu1613), and in the Coprolite Bed at the base of the Speeton Clay, Speeton, North Yorkshire, including BMNH L.19951, L.60190-60193, L.60198-60205.

Diagnosis. Adult shell length 25–30 mm; subovate to subquadrate outline with posterodorsal margin slightly truncate; lunule narrow and deep; oblique internal groove present.

Description. Normal adult shell length 25–30 mm; moderately inflated, thick; inequilateral; commissural outline subcircular to rounded subquadrate; in juvenile specimens shell tends to be more elongate, with distinctly inflated anterior profile; umbo projecting weakly with small sharp beak; anterior margin inflated; posterodorsal margin weakly to moderately truncate; external ornament of c. 1 mm slightly raised commarginal lamellae with finer growth lines in between; weakly defined posterior area, delineated by increased angulation of the commarginal lamellae; lunule very narrow and deep; escutcheon elongate and lanceolate; hinge line well developed (Text-fig. 62) with formula:



TEXT-FIG. 62. Hinge of *Discoloripes fischerianus* (d'Orbigny). Left valve based on BGS Zu712/713 and right valve on BGS Zu714.

Left valve: AIV obscured by lunule development, but appears bluntly lamellar; weakly developed socket in front of 2; 2 cuneiform and vertical and in juveniles is weakly bifid; large triangular socket for 3b; 4b elongate and lamellar, running along the ventral margin of the nymph; posterior laterals obscure, and probably only represented by weak swellings at posterior of hinge; right valve: AIII elongate, blunt and tuberculiform and situated below anterior end of lunule, at ventral margin of hinge; feeble socket in front of 3a; 3a itself subvertical and weak with dorsal end obscured by lunule; large deep triangular socket for 2; 3b strong, opisthocline and distinctly bifid; socket for 4b poorly defined but separating 3b from elevated nymph; posterior laterals obscure or absent.

Shell interior smooth, without pustules; adductor scars deeply inserted in adults, although less

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distinct in juveniles; anterior adductor scar elongate, recurved and isolated from pallial line for most of its length; posterior adductor scar suboval; oblique internal groove present (Pl. 22, figs 10, 17b); shell margin thickened below pallial line and smooth.

Measurements. (In mm, see Text-fig. 60)

	Valve	L	Pp	LE	LLi	LLu	Н	В
BGS Zu694	L	_	_	6	3.5	4	13	3'
Zu695	R	15	10	6	-	_	12	3'
Zu403/4	?	32	19	18	11	8	30	7'
Zu710/11	L&R	13	8	5	_	3	11	5
Zu712/14	R	16	10	7	3	_	13	3'
Zu715	L	30	19	15	_	7	25	6'
Zu730	R	_	-	8	3	5	15	_
Zu817/8	R	30	14	15	9	9	27	- 7'
Zu887	L	34	23	-	_	_	23	7'
Zu4031/2	R	27	20	14	9	7	26	6'
GSM117509	L&R	36	26	12	_	_	-	17

Discussion. Discoloripes fischerianus has been referred to Loripes by Gerasimov (1955, 1969) and to Mesomiltha by Wellnhofer (1964). Both these genera are regarded by Chavan (in Moore (ed.), 1969) as having only a single right valve cardinal tooth. As both 3a and 3b are clearly seen in the Spilsby Sandstone material, the species is here placed in Discoloripes Wellnhofer, 1964. The closely related Jagonoma Chavan, 1946 has more regular surface ornament of alternating weak and strong commarginal lamellae and 3b is not bifid.

Although the specimens, here identified as *Discoloripes fischerianus*, appear identical with Russian Platform material in external appearance, the internal features of the Russian specimens are incompletely illustrated. D'Orbigny's original figure (1845b, pl. 35, figs 31-32) shows no apparent lunule, although in Spilsby specimens it is clearly developed. The specimens illustrated by Gerasimov (1955) include internal moulds with deeply impressed adductor scars and pallial line. They show both smooth and pustulose interiors and oblique grooves, but in the Spilsby specimens only non-pustulose interiors have so far been encountered. A smooth phosphatized internal mould from Mniovniki is illustrated on Plate 21, fig. 17. *Discoloripes lirata* (Phillips, 1829, *sensu* Arkell, 1934) is distinguished by the broader lunule, the less pronounced anterior region and the larger adult size. Fürsich (1982) has illustrated *D. lirata* (as *Discomiltha*) from the Oxfordian and Volgian of East Greenland. The range of characters described is very close to, or even overlaps those of Spilsby specimens of *D. fischerianus*. The precise relationship of these taxa cannot be achieved without population studies based on well preserved specimens.

Discoloripes septentrionalis sp. nov. (see below) is distinguished by its much greater adult size and the Sandringham Sands specimens show a particularly strongly pustulose interior.

Discoloripes? inaequalis (d'Orbigny, 1845b), from the 'Oxfordien' (probably M. Volgian) of the Russian Platform, is superficially very similar to D. fischerianus but may differ in the more obliquely truncate posterodorsal margin. Its hinge is unknown.

'Lucina' concinna (Damon, 1860, pl. 9, fig. 10; BMNH L.6836) from the Kimmeridge Clay of the Weymouth region, originally described as a species of Corbis, appears similar to but is more elongate than D. fischeriana or D. lirata, and the commarginal ornament more widely spaced, but its hinge is unknown. A specimen showing clearly developed external ornament, lunule and escutcheon is figured here (Pl. 21, fig. 18). Although Wignall (1990) referred L. concinna to Mesomiltha, the external ornament contrasts with that genus as interpreted below, being more irregular and the posterior area more differentiated. Another Kimmeridgian taxon, originally referred to Lucina minuscula Blake, 1875, has now been referred to Isocyprina (Venericyprina) by Clausen & Wignall (1990).

Occurrence. Lower Volgian of East Greenland, Spitsbergen; Middle Volgian of eastern England, East Greenland, Russian Platform (Text-fig. 63).



TEXT-FIG. 63. Palaeogeographic distribution of *Discoloripes* fischerianus (d'Orbigny).

Discoloripes septentrionalis sp. nov. Pl. 23, figs 1-5; Text-fig. 64

Name. Latin septentrionalis, northern.

- vp 1936 Lucina sp. nov. aff. L. inaequalis d'Orbigny; Spath, p. 123, pl. 50, fig. 8 only [Middle Volgian, Milne Land, East Greenland; non pl. 46, figs la-b = D. fischerianus (d'Orbigny)].
- v 1936 *Lucina* (?) sp. ind. Spath, p. 124, pl. 48, fig. 7. [Loose block attributed to Portlandian by Spath, but probably Ryazanian, South Jameson Land, East Greenland].
- v 1936 Lucina sp. nov. (?) ind. Spath, p. 124, pl. 50 fig. 9 [Middle Volgian, Milne Land, East Greenland].
- vp. 1947 Lucina aff. fischeriana d'Orbigny; Spath, p. 43, pl. 3, fig. 7 only [Ryazanian, South Jameson Land, East Greenland; pl. 5, fig. 12 is closer to D. fischerianus].
- vp. 1955 Loripes fischerianus (d'Orbigny); Gerasimov, p. 66, pl. 6, fig. 10 only [Middle Volgian, Moscow, central Russian Platform; non figs 4,5,7-10 = D. fischeriana (d'Orbigny)].
- vp 1964 Loripes (Discoloripes) gerasimovi Wellnhofer, p. 81, text fig. 52b only [Middle Volgian, Moscow, central Russian Platform; non fig. 52a, pl. 7, figs 1-5 = D. gerasimovi, Lower Volgian, Bavaria, West Germany].
- vp 1982 Discomiltha lirata (Phillips); Fürsich, p. 67, figs 27B,D [Middle Volgian, Milne Land, East Greenland].
- v 1982 Discomiltha (?) sp. A. Fürsich, p. 69, figs 27C, E [Middle Volgian, Milne Land, East Greenland].

Type specimens. Holotype: MGUH, Kelly Collection MGUH 20350; basal shell bed of the Muslingeelv Member of the Hesteelv Fm., *H. kochi* Biozone, Ryazanian, East bank Muslingeelv, 3 km south of Crinoidbjerg, Jameson Land, East Greenland. 12 paratypes: MGUH 20345– 20349; horizon and locality as for holotype; BGS, CE1929, CE2093-4, CE2100, CE2121, CE2190, *Subcraspedites* band, basal Cretaceous nodule bed, Lower Mintlyn Member, but reworked from Runcton Member, *lamplughi* Biozone, Upper Volgian, Roxham Farm and CE3776 same horizon, flood relief channel, Abbey Station, West Dereham, Norfolk.

Diagnosis. Large lucinid with mature specimens commonly reaching length 65 mm; outline rounded with slightly produced anterior; anterior adductor scar very large, very broad and slightly separated for most of its length from pallial line; oblique internal groove absent.

Description. Shell thick and moderately inflated; mature adults commonly up to length 65 mm, maximum 90 mm; posterior slightly truncated with weakly angular posteroventral junction; anterior slightly produced and deeper than posterior; umbo rounded, low with small sharp prosogyrate beak, weakly overhanging lunular depression in commissural outline; lunule short, asymmetrical and deep, deepest in left valve; escutcheon long and nymph deeply set, although in some Greenland specimens ligament can be seen to be projecting slightly beyond commissural outline; exterior surface ornamented with low irregular growth increments; posterior area scarcely differentiated from flank; hinge line strongly developed (Pl. 23, figs 4, 5; Text-fig. 64) with formula:

RV	(AIII)	(0)	(3a)	0	3b	0	n
LV	(0)	(AIV)	. ,	2	0	4b	n



TEXT-FIG. 64. Internal morphology of *Discoloripes septentrionalis* sp. nov. A, detail of hinge line, left valve based on MGUH 20350 and right valve MGUH 20354. B, internal mould of right valve showing musculature and pallial line, based on MGUH 20349.

Anterior laterals weak; AIII a short blunt swelling below and to anterior of lunule; AIV a low tuberculiform swelling situated directly under anterior of lunule; floor of lunule comes almost down to ventral margin of hinge line in mature specimens, but may be slightly less deeply set in younger individuals; in left valve 2 and 4b are prominent; 2 stoutly cuneiform and subvertical, 4b narrow but strongly opisthocline with relatively prominent groove separating it from long relatively low nymph; in right valve, 3a weak, usually obscured by lunular development; 3b stout and broadly triangular, separated from the nymph by a wide groove; nymph deeply set and elongate; posterior laterals appear to be completely lacking.

Internally shell either smooth (Pl. 23, fig. 1) or coarsely pustulose (Pl. 23, fig. 2); some pustules are sufficiently large to be called tubercles and may be up to 6 mm broad and 3 mm high (Pl. 23, figs 2b, d); no trace of an oblique median groove; adductor scars moderately deeply impressed; anterior adductor scar very long, broad and arcuate, extending almost to ventral part of pallial line, although separated from it for most of its length; posterior adductor scar subcircular to suboval with very slight pallial notch where it joins pallial line; ventral margin smooth; but over much of anterior part of shell interior especially on adductor scar, there may be weak, slightly arcuate, radial striae.

Measurements. (In mm, see Text-fig. 60)

	Valve	L	Lp	Н	В
MGUH 20346	R	92	52	76+	18
20347	L	89+	46+	82	19
20348	L	74	45	72	13
20349	R	78	50	68	15
Holotype: 20350	L	82	56	74+	18
BGS CE2120	L&R*	39	19	37	18
CE2190	L&R*	39	22	35	19
CE2093	L&R*	63	36	58	28
CE 3776	L&R*	66	40	59	29
CE1920	L&R*	66	35	67	28

* Internal moulds, all slightly worn at commissural margins.

Remarks. D. septentrionalis differs from most other Jurassic lucinids by its large size, rounded outline and broad anterior adductor muscle scar. D. gerasimovi Wellnhofer, 1964 has a much narrower anterior adductor scar although both species show it isolated from the pallial line for most of its length. Lucina balmensis Contejean, 1860, from the Calcaire à Corbis, Kimmeridgian of Montbeliard, France, grows as large as D. septentrionalis but has a more distinct broad groove on the exterior running from the umbo to the posterior margin and its dentition is unknown.

Occurrence. Middle Volgian of the Russian Platform; Upper Volgian of eastern England; Ryazanian and possibly Middle to Upper Volgian of East Greenland (Text-fig. 65).



TEXT-FIG. 65. Palaeogeographic distribution of Discoloripes septentrionalis sp. nov.

Genus MESOMILTHA Chavan, 1938

Type species. By original designation; Lucina pulchra Zittel & Goubert, 1861; Sables de Glos, Upper Oxfordian, Calvados, France.

Diagnosis. Outline subovate; shell solid; external ornament of very regular, strong, raised commarginal lamellae which pass onto almost undifferentiated posterior area; ventral margin smooth; hinge narrow with dental formula:

RV	(AIII)	(0)	(3a)	0	3b	0	n
LV	(0)	(AIV)	(0)	2	0	4b	n

Distribution. Lower Jurassic to Lower Cretaceous of Europe.

Mesomiltha biscathorpensis sp. nov. Pl. 21, figs 9–16; Text-fig. 66

Name. After the type locality, Biscathorpe, in Lincolnshire.

Type specimens. Holotype: BGS Thurrell Collection Zm2640, and four paratypes Zm2639, Zm2641-2643, Upper Spilsby Sandstone, *albidum* Biozone, Biscathorpe gravel pit, Lincolnshire; other paratypes: Zu4060, Lower Spilsby Sandstone, *preplicomphalus* Biozone, locality 9, Harrington Hall, Lincolnshire; Zu565/6, Zu708/9 same horizon, locality 10, High Barn sand pit, West Keal; and Zu3758, same horizon, locality 11, Spilsby, Lincolnshire.

Diagnosis. Outline subovate; external ornament of very regular strong commarginal lamellae; posterior area scarcely differentiated from flank; hinge with 2, 3b and 4, weak AIII and AIV.

Description. Medium sized with stout shell and elongate subovate commissural outline; deep rounded anterior region with slightly shallower, tapered posterior; posterodorsal margin straight; umbo slightly projecting with small prosogyrate beak; commarginal ribs regular over flank and posterior area with almost no differentiation; lunule shallow and narrow; escutcheon elongate;



TEXT-FIG. 66. Hinge of *Mesomiltha biscathorpensis* sp. nov. Left valve based on BGS Zm2641 and right valve on BGS Zm2640.

hinge and dentition weak (Text-fig. 66); right valve: 3b subvertical flanked by sockets for 2 and 4; AIII weak and laminar, located on ventral side of hinge below anterior of lunule; left valve: AII short, feeble and mainly obscured by lunule; posterior laterals absent or feebly developed; nymph elongate and straight; in left valve, 2 stout, close to proximal end of lunule; 4 slightly opisthocline; posterior lateral not seen; musculature not seen; ventral margin smooth.

Measurements. (In mm, see Text-fig. 60)

	Valve	L	Lp	Н	В
BGS Zm2639	L&R	24.0	11.0	20.0	11.0
Holotype: Zm2640	R	18.5	9.0	16.0	3.5'
Zm2641	L	18.5	10.0	16.5	4·0′
Zm2642	L	13.5	6.0	12.5	3.0'
Zm2643	R	14.0	6.0	11.5	3.0'
Zu565/566	R	20.0	11.0	17.5	4·5′
Zu3758	L&R	12.5	7.0	10.0	2.0'
Zu4060	L	18.5	10.5	16.0	3.0'

Remarks. M. biscathorpensis sp. nov. is distinguished from all other lucinids from the Spilsby Sandstone and Sandringham Sands by the very regular external ornament and by the three cardinal teeth. Other species of Mesomiltha also occur in the overlying Claxby Ironstone and in the Portland Limestone of southern England but the specimens have not yet been fully studied. M?. kostromensis (Gerasimov, 1955) from the Kimmeridgian of the central Russian Platform, has lower, less regular and feebler commarginal ornament and its hinge is unknown.

Wignall (1990) referred to *Mesomiltha concinna* (Damon) from the Kimmeridge Clay, but the external ornament does not correspond to *Mesomiltha* as interpreted here and is discussed above briefly under *Discoloripes fischerianaus* (See Pl. 21, fig. 18).

Occurrence. Upper Volgian and Upper Ryazanian of the Spilsby Sandstone in eastern England.

Superfamily CRASSATELLACEA Ferrussac, 1822 (nom. transl. Newell, 1965 (ex Crassatellidae Ferrussac, 1822)) Family ASTARTIDAE d'Orbigny, 1844

Remarks. Scarlato & Starobogatov (*in Nevesskaya et al.*, 1971) raised the Astartidae to superfamily level. However, the hierarchy for the family used in the Treatise (Cox & Chavan *in* Moore (ed.) 1969) within the higher taxonomic organization of Pojeta (1971), is followed here.

There has been some discussion as to whether the basic hinge line in astartids should be regarded as being lucinoid, that is with two cardinal teeth in each valve, 3a, 2, 3b, 4b (e.g. Cox & Chavan in Moore (ed.) 1969) or corbiculoid (formerly cyrenoid) with 2a, 1, 2b, 3b, 4b (Cossman & Peyrot, 1912; Schmidt, 1935; Moret, 1940 and Nicol, 1955). The more conventional idea, originally proposed by Bernard (1895) and provisionally followed here, is that the astartids had a lucinoid hinge with 3a and 3b arising from the same lamella, although the formula may be expanded to include 5b. However, there are difficulties e.g. Zakharov (1970, p. 103) believed that

in *Neocrassina* (*Pressastarte*) tooth AI was fused to 3a which contrasts with Bernard's ideas. Such problems can only be resolved by detailed ontogenetic studies which cannot be resolved properly here. Until such studies are made it is felt best to follow here the conventional tooth numbering system of Bernard, thus providing continuity with the studies of Chavan (*in* Moore (ed.) 1969), Duff (1978) and Zakharov (1970).

Kauffman & Buddenhagen (1969) discussed sexual dimorphism in Palaeocene Astarte. They concluded that young astartids with smooth interior ventral margins represented the protandric (male) hermaphroditic forms, while the generally larger denticulated examples represented the females. They also noted that convexity increased in the later growth which was associated with the female stage. Smooth and denticulate margins are seen in most of the genera discussed below. It is possible that in the Nicaniella/Trautscholdia assemblages we are dealing with dimorphism through ontogeny in which the protandric Nicaniella is replaced by the female Trautscholdia.

Subfamily ASTARTINAE d'Orbigny, 1844 (nom. transl. Chavan in Moore (ed.) 1969 ex Astartidae d'Orbigny, 1844)

Zakharov (1970) originally placed *Lyapinella* as a subgenus of *Eriphyla* (Subfamily Eriphylinae, Chavan, 1952b). It is here raised to generic level in the present study and transferred to the Astartinae because of its particularly close relationship with *Neocrassina* which is normally placed in that subfamily (see below).

To facilitate generic identification of members of the Astartinae discussed in this monograph, the following key is proposed:

1. Cardinal teeth striated horizontally, valves co	ompressed 5
- Cardinal teeth smooth, valves moderate	ely to strongly inflated 2
2. Adult shell medium to large size	3
- Small to medium size	4
3. Integripalliate	Neocrassina p. 106
— Weakly sinupalliate	Lyapinella p. 106
4. Convex posterodorsal margin	Nicaniella (N.) p. 120
— Concave posterodorsal margin	N. (Trautscholdia) p. 121
5. Valves extremely compressed	Pressastarte (P.) p. 112
— Valves moderately compressed	P. (Pinguiastarte) subgen. nov. p. 116

Genus LYAPINELLA Zakharov, 1970

Type species. By original designation; Eriphyla (Lyapinella) asiatica Zakharov 1970, p. 113; Upper Jurassic, Middle and Upper Volgian, Northern Urals.

Diagnosis (emended). Medium to large size astartid, thick shelled; subovate with projecting, moderately prosogyrate umbo and beak; hinge strong (Text-fig. 67a) with smooth teeth having dental formula:

RV	0	AIII	3a	Ο	3b	0	n		PIII	
LV	AIV		Ο	2	Ο	4b	n	PII	Ο	(PIV)

Shell interior smooth; ventral margin smooth or denticulated; adductor scars moderately impressed; pallial line moderately sinupalliate.

Remarks. Zakharov (1970) introduced Lyapinella as a subgenus of Eriphyla, but here it is raised to full generic level for the following reasons. Eriphyla sensu stricto differs from Lyapinella by having a more circular commissural outline, with less projecting umbonal region, and teeth 3a and AIII fused (fide Chavan in Moore (ed.) 1969). The type species of Eriphyla is E. umbonata Gabb, 1864 from the Upper Cretaceous of North America. Its precise relationship with Lyapinella is not yet established. Lyapinella is very closely related to Neocrassina with most morphological features, including the hinge, very similar. The principal difference is in the pallial line, which in Lyapinella

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TEXT-FIG. 67. Internal morphology of Lyapinella. A, L. laevis (Phillips), showing hinge teeth numbered according to Bernard (1895), pallial line with sulcus and muscle scars. Left valve based on BGS Zm2363 and right valve based on BGS Zm2542. B, internal mould of Lyapinella asiatica (Zakharov), in dorsal, lateral and anterior views, showing muscle scars and pallial line based on BMNH L.14438.

is moderately sinupalliate and in *Neocrassina* is integripalliate. These sinupalliate forms were recognized by Arkell (1932, p. 231) who noted that 'The "*Neocrassina*" group is continued in the Cretaceous by species with a faint pallial sinus'. However, it now appears that *Neocrassina* became sinupalliate in the Upper Jurassic thus giving rise to *Lyapinella*. The development of siphons necessitated the formation of a pallial sinus suggesting a change in life habit from shallow burrowing to deeper burrowing (Stanley 1968). Integripalliate modern astartids have only simple inhalent and exhalent apertures (Saleuddin 1965), which would have been the condition in *Neocrassina*. Amongst the last *Neocrassina s.s.* are included *N. ovata* (W. Smith, 1817) and *N. orientalis* Zakharov, 1970, both of Kimmeridgian age. Species that belong within *Lyapinella* include *L. saemanni* (de Loriol, 1867) from the Lower and Middle Volgian of northern Europe; *L. duboisiana* (d'Orbigny, 1845b) from Middle Volgian of the Russian Platform; *L. laevis* (Phillips, 1829) from the Speeton Clay; *L. mordvilkoae* (Yanin, 1980) from the Berriasian of the Crimea; *L. transversa* (Leymerie, 1842) and *L. beaumontii* (Leymerie, 1842) from the Neocomian of northern Europe; and *L. obovata* (J. de C. Sowerby, 1822) from the European Aptian.

Lyapinella asiatica (Zakharov, 1970) Pl. 24, figs 1–6, 8; Text-fig. 67B

- 1833 Venus sp. Woodward, p. 39, pl. 1, figs 15, 16 [Diluvial Clay (=Boulder Clay), western Norfolk; almost certainly a Spilsby erratic].
- ?v 1904 Astarte sp. cf. Saemanni de Loriol; Madsen, p. 183, pl. 6, fig. 16. [probably Raukelv Fm, Middle to Upper Volgian, Aucellaelv, East Greenland].
- ?pv 1936 Astarte aff. saemanni de Loriol; Spath, p. 115, pl. 47, fig. 2 only [Aucellaelv, South Jameson Land, East Greenland; figs 1, 3, 5, = L. saemanni (see Fürsich 1982)].
- *v. 1970 Eriphyla (Lyapinella) asiatica sp. nov. Zakharov, p. 114, pl. 14, fig. 11; pl. 15, figs 1-6 [Middle & Upper Volgian, North Urals].
- v. 1974 Eriphyla (Lyapinella) asiatica Zakharov; Zakharov, p. 153, pl. 34, fig. 1 [Middle Volgian, North Urals].
- ?pv 1982 Eriphyla (Lyapinella) saemanni (de Loriol); Fürsich, p. 76 figs P, Q, [Specimens from the Lingula Bed are transitional to L. asiatica; Middle Volgian, Milne Land, East Greenland; non fig. 29, N, 0 = L. saemanni].
 - v. 1987 Eriphyla (Lyapinella) asiatica Zakharov; Besprozvannykh, p. 71 [Museum catalogue].

Type specimens. Holotype: IGGN Zakharov Collection No. 333/479; Strajevskya strajevskyi Subzone, Middle Volgian, River Yatria, north Urals. 146 paratypes: Middle to Upper Volgian of the same area.

Material. c. 300 specimens: including BGS Zu3644, Zu3661, Zu3664, lamplughi Biozone, Upper Volgian, same locality; BGS CE 3469, oppressus Biozone, Upper Volgian, locality 12, Leziate, Norfolk; BGS Zu534, Zu553, Zu866, Zu868, Zu870/871, preplicomphalus Biozone, Upper Volgian, locality 10, East Keal, Lincolnshire.

Diagnosis. Adult large; commissural outline suboval, slightly elongate, with prominent prosogyrate umbo. Surface ornament of strong commarginal ribs usually becoming gradually weaker after c. 15 mm from the umbo.

Description. Shell with adult length usually 40–50 mm; commissural outline usually suboval, variable, but tending towards slightly elongate; moderately inflated; umbo prominent, distinctly prosogyrate; beak small, prosogyrate and incurved; lunule short, lanceolate and deep with floor in left valve overlapping that of right; margins evenly rounded except for slightly obliquely truncate anterodorsal margin; escutcheon elongate, lanceolate with prominent long nymphs; surface ornament of strong commarginal ribs with fine growth lines superimposed, usually becoming gradually weaker after about 15–20 mm. from umbo. Hinge line strong; dental formula as given in generic discussion; left valve AIV bluntly laminar forming floor of lunule; small socket for 3a rather crowded by lunule growth; 2 large and opisthocline, moderately narrow and triangular with deep obliquely triangular socket behind for 3b; 4b bluntly laminar and almost horizontal backing straight onto broad nymph plate; PII and PIV bluntly laminar with latter commarginal with posterior of escutcheon, both situated well behind the nymph plates; deep socket for PIII; right valve AIII bluntly laminar, with deep socket above for AIV; AIII dies out well before 3a which is a triangular projection suspended from proximal end of the lunule floor; deep triangular

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socket for 2; 3b strong prominent opisthocline triangular tooth with a narrow deep and oblique socket for 4b separating it from nymph; nymph plate prominent; single bluntly laminar posterior lateral PIII occupying floor of posterior half of escutcheon, but dying out before reaching nymph; shell interior smooth (Pl. 24, fig. 8; Text-fig. 70b); umbonal cavity large; adductor muscle scars deeply set; pedal retractor scars small and subovoid located on proximal side of adductor muscle scars; pallial line weakly impressed and with small sulcus; margin may be smooth (Pl. 24, fig. 5) or finely denticulate (Pl. 24, fig. 4d, e).

Measurements. (In mm, Text-fig. 60)

									Denticulate
									or
	Valve	L	Lp	LE	LLi	LLu	Η	В	smooth
BGS CE3469	R	42	33	25	12	13	36	10'	S
Zu868	R	44	40	27	16	14	43	10'	S
Zu879/871	L&R	46	36	27	15	14	42	13'	D
Zu3644	R	_	38	28	15		44	_	-
Zu3661	R	33	29	_	-	_	31	_	_

Remarks. In Boreal regions three species of *Lyapinella* occur during the Volgian. The earliest recorded species is L. saemanni (de Loriol, 1867) which occurs in the Anglo-Paris basin, central England (Blake 1880), Denmark erratics (Skeat & Madsen, 1898) and East Greenland (Fürsich 1982), in the lower to early part of the Middle Volgian. It is a relatively short species with more erect umbo than in L. asiatica, and the ribbing is stronger and extends further over the flank. Some specimens are illustrated on Plate 26, figs 11-13, from the Lower Volgian, Shotover Grit Sands of Swindon, Wiltshire. The type species, L. asiatica, hitherto recognized by Zakharov (1974) from the North Urals is here recorded appearing in the oppressus Biozone in eastern England and possibly in the Lingula Bed, Laugeites groenlandicus Biozone of Milne Land, both of late Middle Volgian age. The species continues into the Upper Volgian *lamplughi* Biozone in eastern England. L. saemanni and L. asiatica appear to represent a single lineage in East Greenland (Fürsich, 1982) and England. Fürsich (1982, p. 77) identified L. saemanni in the Lingula Bed, Middle Volgian of Milne Land, but noted that the specimens were more elongate than in the underlying beds, and were transitional towards L. asiatica. L. asiatica was a more elongate form with less projecting umbones. The third species, L. duboisiana (d'Orbigny, 1845b) is very distinct from the first two. It appears at the beginning of the Middle Volgian on the Russian Platform and also is recorded



TEXT-FIG. 68. Palaeogeographic distribution of Volgian Lyapinella: L. asiatica (Zakharov), L. duboisiana (d'Orbigny), and L. saemanni (de Loriol).

occurring in Poland (Lewinski, 1924). It is characterized by a much more regularly, horizontal oval, outline than *L. asiatica* with a low umbo and coarse commarginal ribs which extend over the whole flank. The species was well illustrated by Gerasimov (1955, pl. 5, figs 1–6), but a specimen is also figured here (Pl. 24, fig. 7a–c) from the Middle Volgian of Tatarova near Moscow. The *saemanni-asiatica* lineage is replaced in the Ryazanian by *L. rawsoni* sp. nov. (see below), which is distinguished by having a much smoother exterior from about 10 mm from the beaks. *L. laevis* (Phillips) is a relatively tall species which appears in the *albidum* Biozone and continues into the Valanginian (see below).

The earliest specimens of *Lyapinella* in the Spilsby Basin occur in the Basal Spilsby Nodule Bed but are too incomplete for specific identification (e.g. BGS Zu3644).

Occurrence. Late Middle Volgian to Upper Volgian of eastern England and East Greenland; lower Middle to Upper Volgian of the north Urals and Siberia (Text-fig. 68).

Lyapinella rawsoni sp. nov. Pl. 25, figs 1–16; Pl. 26, figs 9, 10

Name. After Dr. Peter F. Rawson, University of London.

- v. 1947 Astarte cf. saemanni de Loriol; Spath, p. 41, pl. 4, figs 3-4 [Hesteelv Fm, Ryazanian, South Jameson Land, East Greenland].
- v. 1964 Astarte saemanni de Loriol; Sorgenfrei & Buch, p. 131, pl. 7, figs 80-82 [originally dated as Portlandian (but re-evaluated as Ryazanian on dinocyst evidence by Davey, 1982, p. 33), Börglum, Denmark].

Holotype. MGUH, 20342, Basal Shell Bed of the Muslingeelv Member of the Hesteelv Formation, kochi Biozone, Ryazanian, E bank of Muslingeelv, 3 km S of Crinoidbjerg, South Jameson Land, East Greenland.

Paratypes. Abundant, including: MGUH, 20341, 20343, 20344, as for holotype; BGS CE1554, CE1566, CE2458, CE2488, CE3033, CE3041, from the Mintlyn Beds, kochi Biozone, West Dereham, Norfolk. BGS CE4420, CE4507, CE4771, CE4806, CE5433 stenomphalus Biozone, Ryazanian, Mintlyn Wood, Norfolk; BGS BDC1031A, Mintlyn Beds, ?stenomphalus Biozone, Marham borehole, Norfolk.

Diagnosis. Adult shell of medium size, commonly 40-50 mm in length; commissural outline elongately suboval with prominent, moderately to distinctly prosogyrate umbones; surface ornament of strong commarginal ribs up to 10 mm from the umbo, thereafter ribbing becomes feeble.

Description. The shell shape and structures are basically as for L. asiatica but differ in the exterior ornament which consists of strong commarginal ribs usually for the first 10 mm, thereafter becoming very feeble, giving a much smoother general appearance to the shell. A particularly clear cast of the external form of the ligament is shown in Pl. 25, fig. 7.

Measurements. (In mm; see Text-fig. 60)

										denticulate
		Value	т	In	IF	τт;	ττ.,	н	B	or
MOTH	00041	V AIVC	50	ър		10	17	51		
MGUH	20341	L	59	45	32	18	17	51	10	D
Holotype:	20342	R	53	43	30	14	16	51	15'	D
* •	20343	L	42	33	23	13	11	36	12'	D
	20344	R	43	33	25	14	13	38	11'	D
BGS	CE1554	L	36	33		_	14	34	12'	_
	1566	R	37	30	24	11	12	35	_	_
	2458	L	42	36	30	16	16	39	_	D
	2488	L	27	22	16	7	7	24	7'	_
	3033	R	_	-	21	_	_	38	13'	_
	3041	L	36	32	25	11	14	37	14'	_



TEXT-FIG. 69. Palaeogeographic distribution of Ryazanian Lyapinella: L. laevis (Phillips), L. mordvilkoae (Yanin) and L. rawsoni sp. nov.

Remarks. For comparison of *Lyapinella rawsoni* sp. nov. with *L. asiatica* see discussion above. The apparent size discrepancy between the figured *L. rawsoni* sp. nov. from the Mintlyn beds and the Muslingeelv Member is because the larger examples of the former specimens have been damaged during collection and only the smaller ones are sufficiently complete for illustration.

Lyapinella laevis (Phillips, 1829) is distinguished from L. rawsoni by its more erect and more prominent umbones, especially in old individuals. The type of L. laevis came from the Speeton Clay, but well preserved examples occur in the topmost Spilsby Sandstone of Biscathorpe (described below) and in the lower part of the Claxby Ironstone (Valanginian) which were figured by Woods (1905, pl. 16, figs 5-7).

Lyapinella? crimica (Yanin, 1980) (pallial line not seen) and L. mordvilkoae (Yanin, 1980), from the Berriasian of the Crimea are both more circular in commissural outline than L. rawsoni, the hinges are narrower and less strongly developed and the umbones less prominent, with less incurved beaks. The latter species shows a particularly clear pallial sinus (Yanin 1980, pl. 10, fig. 1b).

Occurrence. Ryazanian of eastern England and East Greenland (Text-fig. 69).

Lyapinella laevis (Phillips, 1829) Pl. 26, figs 1–8; Text-fig. 67

- *. 1829 Crassina laevis sp. nov. Phillips, p. 122, pl. 2, fig. 19 [Speeton Clay, Speeton, North Yorkshire].
- . 1835 Astarte laevis Phillips; Phillips, p. 158, pl. 2, fig. 19 [Speeton Clay, Speeton, North Yorkshire].
- 1843 Astarte laevis Phillips; Morris, p. 79 [Speeton Clay, North Yorkshire].
- 1849 Astarte laevis Phillips; Brown, p. 212, pl. 87, fig. 11 [horizon and locality not stated].
- 1854 Astarte laevis Phillips; Morris, p. 187 [Speeton Clay, North Yorkshire].
- 1875 Astarte laevis Phillips; Phillips, p. 328, pl. 2, figs 18, 19 [Speeton Clay, North Yorkshire].
- 1889 Astarte laevis; Brown, p. 106, pl. 87, fig. 11 [horizon and locality not stated].
- v. 1906 Astarte (Eriphyla) laevis Phillips; Woods, p. 115, pl. 16, figs 5-7, pl. 17, fig. 1 [Claxby Ironstone, Benniworth Haven, Lincolnshire].
- . 1924b Astarte laevis Phillips; Gillet, p. 100 [Neocomian, northern England].
- . 1977 Astarte (Eriphyla) laevis (Phillips); Pyrah, p. 247, [Neocomian, Benniworth Haven, Lincolnshire].

Type specimen. Untraced, Williamson Collection, Speeton Clay, Speeton, North Yorkshire. Material. 25 specimens: BGS Zm2361-2364, Zm23667-2368, Zm2542, ZM2599, Zm2601, Zm2603-2605, Zm2607-2608, Zm2610-2612, Zm2614-2616, Zt3217, Zt3241, Zt3243, Zt3268, Upper Spilsby Sandstone, albidum Biozone, Biscathorpe gravel pit, Louth, Lincolnshire.

Diagnosis. Short and inflated, with marked greater height than length in adult; in late growth stage, exterior is nearly smooth, apart from growth lines.

Description. Medium sized, thick shelled Lyapinella, slightly longer than tall, moderately inflated; commissural outline subovate to trigonal, slightly tall, with slightly projecting prosogyrate umbo and small beak; commissural margin broadly rounded at posterior and more tightly rounded at anterior, and concave in lunular region; exterior ornament of regular commarginal ribs with fine growth lines superimposed; hinge and interior (Pl. 26, figs 1c, 3a, c, 6a) as for L. asiatica; margin smooth (Pl. 26, figs 1, 2) in all small specimens, but occasionally up to 34 mm length, becoming denticulated (Pl. 26, figs 3, 6) in most larger specimens, but the smallest being 17.5 mm.

Measurements. (In mm, seee Text-fig. 60)

						denticulate
						or
	Valve	L	Lp	Н	В	smooth
BGS Zm2361	L	25.0	15.0	22.5	7.0	S
Zm2362	L	19.5	10.0	18.0	5.5	S
Zm2363	L	23.0	3.0	20.5	6.0	S
Zm2364	R	17.5	12.5	15.5	$5 \cdot 0$	D
Zm2367	R	21.5	15.0	19.0	6.0	S
Zm2368	R	25.0	16.0	22.0	7.5	S
Zm2542	R	25.0	16.0	23.0	7.0	D
Zm2599	L	32.0	19.0	29.0	9.0	S
Zm2601	L	30.0	20.0	28.0	9.5	S
Zm2603	L	25.0	16.0	24·0	8.5	S
Zm2604	R	41·0	28·0	37.0	12.0	D
Zm2607	L	33.0	23.0	31.0	8.0	S
Zm2608	L	35.0	21.0	34.0	11.0	D
Zm2610	L	43 ·0	30.0	41·0	13.0	D
Zm2611	L	34.0	21.0	31.0	10.0	S
Zm2612	L	35.0	25.0	33.0	11.0	D
Zm2614	R	37.0	27.0	34.0	12.0	D
Zm2615	L	33.0	22.0	31.0	10.0	D
Zm2616	R	32.5	21.0	29.0	9.0	D
Zt3217	R	37.0	23.0	35.0	11.0	D

Remarks. The specimens of this species are very much better preserved than the previously described species of *Lyapinella* from the Spilsby Basin (see above). The specimens are similar to, but slightly smaller, than those figured by Woods (1906) (SMC B.11357-11359) from the Claxby Ironstone of Benniworth Haven. The whole of the Claxby Ironstone at the site from where Woods' specimens were collected (locality 4) is of Lower Valanginian age (Kelly & Rawson 1983). *Lyapinella* from the upper part of the Claxby Ironstone are of Hauterivian age and include the *L. transversa—beaumontii* group of Leymerie (1842) which has much more prosogyrate umbones with a very short anterior.

Occurrence. Upper Ryazanian and Lower Valanginian of eastern England (Text-fig. 69).

Genus PRESSASTARTE Zakharov, 1970

(Syn. Anabarella Zakharov, 1970, non Vostokova, 1962)

Type species. By original designation; Astarte trembiazensis de Loriol, 1901 (Zakharov, 1970, p. 103); Oxfordian of the Jura Bernois. Interpreted here as a junior subjective synonym of Astarte striatocostata Münster in Goldfuss & Münster, 1837.

Diagnosis (emended). Small-medium sized astartid; compressed and thick shelled; commissural outline subcircular-subovate with small projecting prosogyrate umbo and almost coincident beak; hinge line strong with formula as in *Lyapinella*, but cardinal teeth striated; ventral margin smooth or crenulated; pallial line integripalliate. Dental formula (Text-fig. 70B):

RV	AIII	0	AV	3a	0	3b	0	n		PIII	
LV		AIV		0	2	0	4b	n	PH	0	PIV

Discussion. The subgenera Pressastarte and Anabarella were introduced by Zakharov (1970) as divisions of Neocrassina, although Anabarella was preoccupied by the name originally introduced by Vostokova (1962) for a monoplacophoran. Anabarella Zakharov was originally differentiated from Pressastarte by its 'larger, more regular shape and its distinctive oval-rounded outline'. Zakharov included Astarte senecta Woods, 1906 from the Claxby Ironstone in Pressastarte. P. senecta has been examined together with the type species of Anabarella Zakharov, 1970 (A. vai Krimgolts in Krimgolts et al., 1953; holotype: TSNIGR 286/5393). Both species show shape, external ornament and dentition identical to those of Pressastarte. Because Anabarella Zakharov can be accommodated within Pressastarte, there is no need to rename that subgenus.

Zakharov (1970) listed several Jurassic and Cretaceous species from western Europe that he placed in *Pressastarte*, and the name is gaining rapid acceptance by western palaeontologists (e.g. Duff 1978; Fürsich 1982; Wignall 1990).

The principal differences between *Lyapinella* and *Pressastarte* are that the latter is generally much smaller and more compressed, the umbonal cavity is very reduced, PIV is less differentiated from the nymph, the lunule is less excavated and the pallial line is integripalliate. In addition there are features in *Pressastarte* which, hitherto, have been unrecognized in astartids. These are in the form of horizontal striations on the cardinal teeth which are shown in Text-fig. 70. They occur on the anterior and posterior of 2 and 3b, the anterior of 4b and the posterior of 3b. Being perpendicular to the commissure they would assist the valves to be closed accurately.



TEXT-FIG. 70. Internal morphology of Pressastarte (Pinguiastarte) pressula Zakharov. A, hinge with teeth numbered according to Bernard (1895), pallial line and muscle scars, left valve based on BGS Zu549/560 and right valve Zu555/556. B, detail of hinge showing horizontal striations on the cardinal teeth, left valve based on SMC J.15813 and right valve based on J.15158, Swindon Clay, Middle Volgian, Swindon, Wiltshire.

Examination of some astartid specimens in the BGS collection indicates that Pressastarte may be related to Neocrassina s.s. Some specimens of N. ovata (W. Smith) from the Kimmeridgian show a distinct change in growth style at 15–20 mm from the umbo. Up to this point the shell is usually strongly compressed and smooth with the general exterior features of P. striatocostata; thereafter the features of the adult shell of Neocrassina s.s. appear, where the shell becomes more elongate and inflated. This change in ornament is related to the protandrous hermaphroditic state which is discussed further below under the Family Astartidae. Chavan (1952a) has already commented on the similarities of the young state of N. ovata with species that are here referred to Pressastarte, e.g. P. nummus (Sauvage & Rigaux) and P. pelops (d'Orbigny). Juveniles of Neocrassina and Lyapinella which have been examined so far, do not bear horizontal striations on the cardinal teeth. The precise relationship between Neocrassina s.s. and Pressastarte is not resolved and requires further study. Pressastarte is raised therefore to full generic level and is further subdivided into two subgenera, Pressastarte (P.) and P. (Pinguiastarte) subgen. nov.

Subgenus **PRESSASTARTE** Zakharov, 1970

Diagnosis. Pressastartid having feeble to weakly inflated shell, with coarse ribbing close to the umbo only.

Remarks. Pressastarte (P.) is differentiated from P. (Pinguiastarte) subgen. nov. by its extremely compressed shell. Typical species include P. striatocostata (Münster in Goldfuss & Münster, 1837) (including P. trembiazensis (de Loriol, 1901), described below, P. ungulata (Lycett, 1863) from the Cornbrash of Yorkshire and P. calvertensis Duff, 1978 from the Lower Oxford Clay of Buck-inghamshire. For discussion of the last two species see Duff (1978, p. 93).

Occurrence. Callovian to Ryazanian of Europe.

Pressastarte (Pressastarte) striatocostata (Münster, in Goldfuss & Münster, 1837)

Pl. 27, figs 2, 3, 5

- *p. 1837 Astarte striato-costata sp. nov. Münster, in Goldfuss & Münster, p. 192, pl. 134, fig. 18a, 6 only [Upper Jurassic, Hannover, Germany; non fig. c = holotype of P. pelops d'Orbigny, 1850a].
- non 1844 Astarte striato-costata sp. nov. d'Orbigny, p. 64, pl. 262, figs 7–9 [Neocomian Aube, Haute Marne, Yonne, France; junior homonym].
- . 1850a Astarte Philea sp. nov. d'Orbigny, p. 363 [Oxfordian, Neuvizi, Ardennes and Trouville, Calvados, France].
- . 1850b Astarte Cepha sp. nov. d'Orbigny, p. 50 [Kimmeridgian, Villerville, Calvados, France].
- p. 1863 Astarte striato-costata Münster; Goldfuss & Münster, p. 183 [Upper Jurassic, Lubke, Germany].
- . 1863 Astarte trigonarium sp. nov. Dollfus, p. 62, pl. 15, figs 12-13 [Kimmeridgian, Cap de la Hève, France].
- *p. 1882 Astarte depressa Münster; Roeder, pl. 4, fig. 3a only [Oxfordian, Alsace; non fig. 5c = P. depressa (Münster)].
 - . 1883 Astarte striato-costata Goldfuss; Lahusen, p. 31, pl. 2, fig. 26 [Oxfordian, Novoselki, Ryazan, central Russian Platform].
 - . 1901 Astarte trembiazensis sp. nov. de Loriol, p. 69, pl. 4, figs 24-26 [Oxfordian, Jura Bernois, Switzerland].
 - . 1904 Astarte trembiazensis de Loriol; Ilovaisky, p. 256, pl. 9, figs 7-9 [Oxfordian, central Russian Platform].
 - . 1911 Astarte trembiazensis de Loriol; Boden, p. 62, pl. 3, fig. 11 [Lower Oxfordian, Lithuania].
- vnon 1911 Astarte striato-costata Münster; Ravn, p. 471, pl. 33, fig. 11 [Kimmeridgian, Store Koldeway, East Greenland; more inflated than P. striatocostata].
 - . 1927 Astarte Philea d'Orbigny; Cottreau p. 49, pl. 46, figs 1, 2 [Oxfordian, Ardennes, France].
 - . 1931 Astarte Cepha d'Orbigny; Cottreau, p. 192, pl. 65, figs 15, 16 [Kimmeridgian, Calvados, France].
 - . 1952 Astarte striatocostata Goldfuss; Makowski, p. 9, pl. 5, fig. 5; text-fig. 2 [Oxfordian, Poland].
 - . 1955 Astarte trembiazensis de Loriol; Gerasimov, p. 60, pl. 4, fig. 16 [Oxfordian of Ryazan, central Russian Platform].
 - . 1970 Neocrassina (Pressastarte) trembiazensis (de Loriol); Zakharov, p. 104, pl. 13, figs 9-11 [Oxfordian, Moscow; Callovian, Lithuania].
 - . 1981 Nicaniella trigoniarum (Dollfus); Rioult, p. 44 [Calcaire à Trigonies, Lower Kimmeridgian, north France].
 - v. 1987 Neocrassina (Pressastarte) trembiazensis (de Loriol); Besprozvannykh, p. 119 [Museum catalogue].

Type specimens. The original specimens came from the Upper Jurassic, 'Jurakalk bei Lubke' near Hannover, Germany. Untraced. Subsequently d'Orbigny (1850a, p. 363) designated the

original of Goldfuss & Münster, pl. 134, fig. 18c (only) as a syntype of Astarte pelops which is here regarded as Pressastarte (Pinguiastarte) pelops.

Material. 3 specimens: BGS Zm2369, Zm2371-2, Upper Spilsby Member, albidum Biozone, Upper Ryazanian, Biscathorpe gravel pit, Louth, Lincolnshire.

Diagnosis. Strongly compressed pressastartid with coarse commarginal ornament up to 4 mm from beak, which dies out on more distal flank.

Description. Very compressed, medium sized with subcircular outline with straight to feebly indented anterodorsal margin; umbones and beaks coincident, slightly projecting and weakly prosogyrate; strong commarginal ribs with fine growth lines superimposed continue for c. 5 mm from beaks; rest of flank smooth with fine growth lines only; lunule shallow, elongate and lanceolate; escutcheon very elongate and narrow; interior smooth, integripalliate with crenulate ventral margin; umbonal cavity minute; hinge stout (only right valve seen); 3a subvertical, 3b slightly opisthocline, both prominent and striated with deep socket for 2; AV commarginal with floor of lunule and AIII at ventral edge of hinge, both bluntly laminar and separated by elongate groove for AIV; nymph small; PIII elongate with feeble grooves above and below for PII and PIV (Text-fig. 70).

Measurements. (In mm, see Text-fig. 60).

						denticulate
						or
	Valve	L	\mathbf{Lp}	Н	В	smooth
BGS Zm2369	L&R	11.0	6.0	11.0	4 ∙5	D
Zm2371	L	11.0	8.0	11.5	2.5	S
Zm2372	L&R	10.5	7.0	10.5	4 ·0	S

Remarks. Externally Pressastarte striatocostata is very similar to P. ungulata (Lycett, 1863) from the Cornbrash of Yorkshire and P. calvertensis Duff, 1978 from the Lower Oxford Clay, however, the hinges of the last two species differ in their more delicate structure and especially in their less prominent cardinal teeth. P. lincolnshirensis sp. nov. (see below) is distinguished by its more elongate shape and slightly differentiated posterior area.

Occurrence. Oxfordian of France, Germany, Switzerland, Lithuania, central Russian Platform; Kimmeridgian of north France; Upper Ryazanian of eastern England (see Text-fig. 71).



TEXT-FIG. 71. Palaeogeographic distribution of *Pressastarte* (*Pressastarte*) striatocostata (Münster).

Pressastarte (Pressastarte) lincolnshirensis sp. nov. Pl. 27, figs 1, 4

Name. After the county of Lincolnshire.

Type specimens. Holotype: BGS Thurrell collection Zt3270, Upper Spilsby Member, albidum Biozone, Ryazanian, Biscathorpe gravel pit, Louth, Lincolnshire; paratype, BGS Zm2311, same horizon and locality.

Diagnosis. Pressastartid with commisural outline elongate; strong commarginal ribbing extends only 4 mm from the beak; posterior area slightly demarcated.

Description. Shell medium sized, very compressed and subovate in outline; umbo and beak slightly projecting and weakly prosogyrate; posterodorsal margin straight and anterodorsal margin straight to feebly concave; both lunule and escutcheon shallow, elongate and narrowly lanceolate; exterior ornamented by five major commarginal ribs with subordinate growth lines reaching about 4 mm from beak; rest of flank smooth except for growth lines; posterior area feebly defined by weak angulation in growth lines; interior smooth; ventral margin smooth and thin or thick and crenulate; adductor muscle scars slightly impressed on their dorsal sides; pallial line entire; hinge well developed; 2 stout, acutely triangular, striated and subvertical; 4b acutely triangular, striated, opisthocline and located on anteroventral edge of small nymph plate; prominent cavities for 3a and 3b; AII concurrent with ventral margin of lunule; PII and PIV bluntly laminar and elongate, separated by prominent groove for PIII.

Measurements. (In mm, see Text-fig. 60).

						denticulate
						or
	Valve	L	Lp	Н	В	smooth
BGS Zm2311	R	13.0	9.0	12.0	3.0'	D
Holotype Zt3270	L	13.0	7.5	11.0	2.5'	S

Remarks. See P. striatocostata.

Occurrence. Upper Ryazanian of eastern England.

Subgenus **PINGUIASTARTE** nov.

Name. Latin pinguis, stout.

Type species. By original designation herein Astarte senecta (Woods, 1906), Claxby Ironstone, Lower Valanginian, Benniworth Haven, Lincolnshire and Speeton Clay, North Yorkshire.

Diagnosis. Pressastartid with only weak to moderately inflate valves, having coarse persistent, commarginal ribbing over most of the flank.

Remarks. The new subgenus Pinguiastarte differs from Pressastarte (P.) by its more inflated shell and the maintenance of coarse commarginal ornament throughout adulthood. Typical species include P. depressa (Münster, in Goldfuss & Münster, 1837), Bathonian, Germany; P. pelops (d'Orbigny, 1850a), Oxfordian, France; P. depressioides (Lahusen, 1883), Oxfordian, Russian Platform; P. pressula Zakharov, 1970, Volgian, North Urals, Russia and eastern England; P. tectiformis (Trautschold, 1866b), Callovian, central Russian Platform.

Distribution. Bathonian-Valanginian, Europe, Greenland, Spitsbergen, Urals, East Africa, Japan.

Pressastarte (Pinguiastarte) pressula Zakharov, 1970. Pl. 27, figs 6–13; Text-fig. 70.

- v. 1970 Neocrassina (Pressastarte) pressula sp. nov. Zakharov, p. 105, pl. 13, fig. 6 [Middle Volgian, North Urals, Russia].
- v 1970 Neocrassina aff. pressula sp. nov. Zakharov, p. 106, pl. 13, fig. 7, [Middle Volgian, North Urals, Russia].
- v 1970 Neocrassina (Pressastarte) sp. Zakharov, p. 106, pl. 13, fig. 8 [Middle Volgian, North Urals, Russia].
- v. 1974 Neocrassina (Pressastarte) pressula Zakharov; Zakharov, p. 153, pl. 33, fig. 4 [Middle Volgian, North Urals, Russia].
- v. 1987 Neocrassina (Pressastarte) pressula Zakharov; Besprozvannykh, p. 119 [Museum catalogue].

Holotype. By original designation; IGGN No. 333/461 Neocrassina (Pressastarte) pressula Zakharov, 1970, p. 105, pl. 13, fig. 6; Dorsoplanites maximus Biozone, Middle Volgian, section 18, R. Yatria, north Urals, Russia.

Material. BGS, including: Zu2008–9, Zu2052, Zu2059/60, Zu2069, Zu2107, Basal Spilsby Nodule Bed, Middle Volgian, locality 3, Nettleton, Lincolnshire; Zu283 oppressus Biozone, Middle Volgian, locality 12, Leziate, Norfolk; Zu549/560, Zu555/556 preplicomphalus Biozone horizon, locality 10, High Barn sand pit, West Keal, Lincolnshire.

Diagnosis. Small sized pinguiastartid, compressed; subovate commissural outline in juvenile becoming subcircular in adult; flank ornament of coarse commarginal ribs overall and especially coarse near the umbo.

Description. Outline rounded, slightly elongate in younger specimens and more circular in large specimens; beaks and umbones prosogyrate and coincident, with slightly indented anterodorsal margin; umbonal angle c. 120°; exterior ornamented by coarse commarginal ribs, the first four being widely spaced and thereafter becoming much closer; posterior area not differentiated; escutcheon deep and lanceolate; lunule slightly more broadly lanceolate and shorter; interior smooth with crenulate or smooth ventral margin; adductor scars moderately impressed; pallial line entire; umbonal infilling bulbous; hinge stout, with 2 acutely triangular and slightly opisthocline; 4b elongate and opisthocline at anteroventral margin of the short nymph plate, both striated; major socket for 3b and minor socket for 3a; AIV slightly recurved and contiguous with floor of lunule; PII and PIV elongate and separated by deep socket for PIII; 3a subvertical and located close to lunule but not contiguous; 3b acutely triangular, opisthocline and separated from nymph by groove; AV feeble and contiguous with floor of lunule, AIII at ventral edge of hinge, both slightly recurved; PIII elongate and bluntly laminar.

Measurements. (In mm, see Text-fig. 60)

						denticulate
						or
	Valve	L	Lp	Н	В	smooth
BGS Zu549/550	L	16.5	12.5	17.0	_	D
Zu555/556	R	14.0	11.0	13.0	4·0	D
Zu2009/2010	R	14.0	10.0	12.0	4.0	D
Zu2059/2060	L	14.5	13.0	11.5	4.5	D

Remarks. Other specimens which are probably conspecific with Pressastarte (Pinguiastarte) pressula occur in the Hartwell Clay of Buckinghamshire (SMC J.1813-9). There are a number of species that are very closely related. P. depressa (Münster in Goldfuss & Münster, 1837, pl. 134, fig. 14) from the Bathonian of Germany has more gradual change from the umbonal ribs to those on the rest of the flank. P. pelops (d'Orbigny, 1850a, p. 363) from the Oxfordian of Germany and France (probable synonyms include Astarte nummus Sauvage & Rigaux, 1871, p. 357; 1872 pl. 8 fig. 5, Oxfordian, Boulonnais and A. pyrene d'Orbigny (1850a, p. 363), Oxfordian, Doubs), has a more rectangular umbonal angle and the ribbing is similar to P. depressa. Fürsich (1982, pl. 29, figs J, K, L) recorded P. pelops from the Middle Volgian of Milne Land, East Greenland. P. depressoides (Lahusen, 1883, pl. 2, fig. 27) and also figured by Gerasimov (1955, pl. 4, figs 10-15) from the Oxfordian of the Russian Platform, has a more erect umbo and slightly finer ribbing.

A specimen figured as Astarte (A.) cf. nummus Sauvage, by Birkenmajer & Pugaczewska (1982) from the mid-Kimmeridgian of Myklegardfjellet, Spitsbergen, appears slightly elongate with a particular elongate posterior, having anastomosing commarginal ribs. The specimen is unlikely to be *Pressastarte* and may represent *Prorokia*, which has been illustrated from a similar horizon in Milne Land, East Greenland by Fürsich (1984a, figs 15, 16).

Occurrence. Middle to Upper Volgian of Eastern England; Middle Volgian of North Urals (Text-fig. 72).



TEXT-FIG. 72. Palaeogeographic distribution of Pressastarte (Pinguiastarte) pressula Zakharov.

Genus NICANIELLA Chavan, 1945

Type species. By original designation; Astarte communis Zittel & Goubert, 1861, p. 201, pl. 2, figs 2-4; Lower Kimmeridgian, Boulonnais, northern France.

Diagnosis. Small, moderately to strongly inflated, weakly prosogyrate; one principal cardinal tooth 3b subcentral in right valve; two principal cardinal teeth in left valve 2, 4b.

Remarks. Chavan (1945; *in* Moore (ed.) 1969) stated that there was no 3a present in *Nicaniella* sensu lato, which embraced also the subgenus *Trautscholdia* Cox & Arkell, 1948. However, in describing the type species, Chavan (1952a, p. 59) indicated that there was a trace of 3a embedded in the lunule. Chavan (1952b) even recorded the presence of 6b, but that has not been seen during the present study. Duff (1978, p. 97) regarded the presence of 3a as typical of *Trautscholdia* s.s. However, specimens regarded here as *Trautscholdia* are those which have distinctly constricted and inflated umbones. The absence or presence of 3a is not a critical feature for separation of the subgenera.

The full dental formula for Nicaniella s.l. is as follows:

RV	AIII	0	\mathbf{AV}	(3a)	0	3b	Ο	(5b)	(O)	n	PIII	
LV		AIV	(O)		2	0	4b	(O)	(6b)	n	PII	PIV

The specimens examined during this study, have well developed anterior and posterior lateral teeth. However, of the cardinal teeth, only 2, 3b and 4b are strong and have deep sockets. 3a may be present weakly or absent due to lunule development. 5b is small but usually present. In Nicaniella s.s. (Text-fig. 73a) 3a may be absent or present. In N. (Trautscholdia) it is almost always absent because growth of the lunule has obscured the site of development. The most obvious feature for distinguishing the difference between Nicaniella and Trautscholdia was recognized by Chavan (in Moore (ed.) 1969). Nicaniella has a convex to straight posterodorsal margin, while in Trautscholdia it is distinctly concave, and the umbo is distinctly constricted and inflated.

Although the above definitions make it easy to allocate individual specimens to one subgenus or the other, the naming of species assemblages from particular horizons is not clear cut. It is possible to find a single species assemblage spanning the subgeneric boundaries. Such assemblages have been illustrated, e.g. Astarte multiformis Roeder, 1882, from the Oxfordian of Alsace. A. multiformis s.s. is a normal Nicaniella (N.), but A. multiformis var. inaequistriata Roeder, 1882 is referred here to N. (Trautscholdia). The bulk of the specimens shown belong to Nicaniella s.s., while some labelled var. inaequistriata have the distinct concave posterodorsal margin of Trautscholdia.



TEXT-FIG. 73. Sketch of morphology of Nicaniella. A, Nicaniella (Nicaniella) supraextensa (Zakharov), showing convex posterodorsal margin, depressed umbonal region and hinge teeth numbered according to Bernard (1895), left valve based on BGS Zu3229 and right valve on BGS Zu2058. B, Nicaniella (Trautscholdia) claxbiensis (Woods) with straight to concave posterodorsal margin and swollen umbonal region, left valve based on BGS Zm2719 and right valve based on BGS Zt3271.

Duff (1978) referred Astarte carinata (Phillips, 1829), from the Oxford Clay of Scarborough, and Astarte phillis d'Orbigny, 1850b, Oxfordian, Neuvizy, France, to the subgenus Trautscholdia. However, his interpretation of each species includes forms of Nicaniella with both constricted and non-constricted umbonal regions. It is usually possible to allocate individual specimens illustrated by Duff (1978) and Roeder (1882), as well as from the Spilsby Basin to one subgenus or the other without difficulty. It is felt here more useful to retain a restricted morphological definition of the subgenera of Nicaniella until a clearer idea of the variation in populations of the genus can be obtained. All the Oxfordian representatives of N. (Trautscholdia) as interpreted here probably belong within the species group of N. (T.) cordata (Trautschold, 1860; Text-fig. 75), the type species for the subgenus, but which may be junior subjective synonym of N. (T.) carinata (Phillips, 1829) (non A. carinata d'Orbigny, 1844 (junior homonym) = A. acuta d'Orbigny, 1847).

Some authors, e.g. Zakharov (1970) place Nicaniella within the Recent genus Astarte (type species: A. scotica (Maton & Rackett, 1807)). The two genera are similar but Astarte s.s. is distinguished here as being more prosogyrate with the cardinal teeth 4b and 3b more opisthocline and 2 close to vertical. In Nicaniella 3b is vertical and axial to the whole shell with 2 and 4b flanking it closely.

A close relative of *Nicaniella* is *Siungiudella*, with the type specimen originally described as *Neocrassina* (*Siungiudella*) *parvula* Lutikov, 1984, from the Upper Pliensbachian of the Syungyude River, east Siberia. The holotype is very similar to *Nicaniella* (*N.*), but lacks the coarse commarginal ornament. Two of the paratypes (Lutikov 1984, pl. 22, figs 5,6) show a distinct anterior elongation of the shell, with increased inflation of the posterodorsal margin, and almost straight to weakly indented anterodorsal margin.

Subgenus NICANIELLA Chavan, 1945

Diagnosis (emended). Small astartid, trigonal to subquadrate in commarginal outline with moderately prominent umbones; anterodorsal margin concave; posterodorsal margin weakly convex to straight; dental formula as given above with 3a weakly developed or absent.

Nicaniella (Nicaniella) supraextensa (Zakharov, 1970) Pl. 27, figs 14–19; Text-fig. 73A

- ? 1861a Astarte Voltzii Goldfuss; Trautschold, p. 81, pl. 7, figs 5a-d [non Goldfuss; syntype of Gouldia mniewnikensis Milashevits, Mniovniki, Russian Platform].
- ? 1861a Astarte minima Phillips; Trautschold, p. 82, pl. 7, fig. 6 [non Phillips; syntype of Gouldia mniewnikensis Milashevitz, Mniovniki, central Russian Platform].
- p? 1881 Gouldia mnewnikensis sp. nov. Milashevits, p. 114 Oxfordian, Mniovniki, central Russian Platform].
- 1955 Astarte mnevnikensis Milashevits; Gerasimov, p. 63, pl. 4, figs 1-4 [Middle Volgian, Russian Platform].
- ? 1969 Astarte mnevnikensis Milashevits; Gerasimov, p. 75, pl. 6, figs 7, 8 [Oxfordian, central Russian Platform].
 v. 1970 Astarte (Astarte?) supraextensa sp. nov. Zakharov, p. 92, pl. 10, figs 10–16 [non Phillips; Kimmeridgian, North
- Urals, Russia].
- v. 1987 Astarte (Astarte?) supraextensa Zakharov; Besprozvannykh, p. 119 [Museum catalogue].

Type specimens. Holotype: IGGN No. 333/400, and 40 paratypes including IGGN 333/401-431, Lower Volgian, Eosphinctoceras magnum Biozone, North Urals, Russia.

Material. 37 specimens: including BGS Zu2058, Zu2061/2062, Zu2103-2105, Zu2108/2109, Basal Spilsby Nodule Bed, locality 3, Nettleton, Lincolnshire.

Diagnosis. Small nicaniellid, ovate to subtrigonal, umbo and beak slightly prosogyrate, adult with c. 10–14 coarse commarginal ribs.

Description. Shell small with maximum adult shell length just in excess of 14 mm; specimens usually 10-12 mm in length; juvenile shell strongly inflated but degree of inflation decreases with age; outline subtrigonal and weakly prosogyrate in adults though tending to be more distinctly prosogyrate in young specimens; posterior bluntly rounded and anterior slightly more acutely rounded; beaks small and prosogyrate, slightly incurved; anterodorsal margin straight; lunule cordate and shallowly impressed; escutcheon elongate and broadly lanceolate; surface ornament comprises c. 10–14 coarse commarginal ribs, trigonal to slightly rounded in cross section, with fine growth lines superimposed; hinge line strong (Text-fig. 75) immediately under the beaks, but weaker in region of lateral teeth; left valve AIV laminar and commarginal with the lunule floor; weak groove for 3a; 2 strong and triangular reaching ventral margin of hinge line; deep triangular socket for 3b; 4b strong but obliquely triangular to laminar, also reaching ventral margin of hinge; 4b backs onto the nymph which is approximately same length and slightly depressed; PII and IV very elongate and laminar, separated by socket for PIII; PIV confluent with escutcheon and almost runs into nymph, but is slightly raised above it, right valve AIII and AV together with socket for AIV are laminar and slightly concave, paralleling lunule floor with which AV is commarginal; 3a usually represented by fine laminar ridge on proximal end of lunule margin, also under lunule a weak buttress may be seen which may represent basal part of the tooth; large deep triangular sockets for 2 and 4b symmetrically placed in front and behind prominent erect triangular 3b; nymph and 5b barely separated from single posterior lateral PIII which is commarginal with escutcheon margin; internally shell smooth; short bulbous umbonal cavity; subequal adductor scars are deeply impressed at their dorsal margins and slightly elevated at the ventral edges; integripalliate; margin may be smooth or denticulate.

Measurements. (In mm, see Text-fig. 60)

x <i>y</i>	0	,				denticulate
						or
	Valve	L	Lp	Н	В	smooth
BGS Zu2061/2	L&R	10	7	9	8	D
Zu2072	L	12	7.5	12	_	D
Zu2104	L	11	9	10	_	S
Zu2105	R	12	8	10	4'	?
Zu2108/9	L	_	_	11	5	D



TEXT-FIG. 74. Palaeogeographic distribution of Nicaniella (Nicaniella) supraextensa (Zakharov).

Discussion. Nicaniella (N.) extensa (Phillips, 1829), from the Oxford Clay of Yorkshire, as revised by Arkell (1934, p. 238) and including N. (N.) mysis (d'Orbigny, 1850b), from the Kimmeridgian of Le Havre, France, (see also Clausen & Wignall 1990, p. 127, pl. 7, figs D–F) has a more prominent posterior and weakly developed angulation of the commarginal ribs over the posterior carinal region. N. (N.) supraextensa differs in its more central umbo and more rounded posterior, lacking the angulation of the commarginal ribs.

Middle Volgian Nicaniella from the Russian Platform have only been figured by Gerasimov (1955) as Astarte mnevnikensis Milashevits. The specimens are smaller than the Spilsby ones and may belong to the same species. Milashevits erected Gouldia mnewnikensis with syntypes based on particular figures of Astarte buchiana d'Orbigny, 1845b, Astarte voltzii Goldfuss (Trautschold 1861a) and A. minima Phillips (Trautschold 1861a). Trautschold's figures differ distinctly from d'Orbigny's. A. buchiana has a distinctly truncate posterior, and Zakharov (1970) placed it in the subgenus Carinastarte? Hinsch, 1953, while the figures of A. voltzii and minima show a more circular outline and strong ribbing. Trautschold's specimens are very small and came from the 'dark sands of Mniovniki'. Gerasimov (1955) regarded Milashevits' species to be of Middle Volgian age and has also excluded d'Orbigny's figure from the synonymy list. The specimens that he figured (1955, pl. 4, 1–4) have a strongly inflated shell and coarse ribbing. They are generally much smaller than fully grown Spilsby Sandstone examples, although small Spilsby Sandstone specimens appear identical.

N. (N). gibba (Gerasimov, 1955) from the Lower Kimmeridgian of Fokino, Bryanskoy Oblast, Russian Platform, is very small and extremely inflated, but has low unconstricted umbones.

Occurrence. Middle Volgian of eastern England and the Russian Platform; Lower Volgian of the north Urals (Text-fig. 74).

Subgenus TRAUTSCHOLDIA Cox & Arkell, 1948

Type species. By original designation; Astarte cordata Trautschold, 1860, p. 347; nom. nov. for A. cordiformis Rouillier & Vossinsky, 1847 pl. D, fig. 15a-h, labelled and described 1848, p. 275 (non A. cordiformis Deshayes, 1830); Oxfordian, central Russian Platform. Eichwald (1868, p. 615) regarded A. cordata as a junior subjective synonym of A. gryphaeoides Fahrenkohl, 1844, p. 798, but this in turn is recognized here a junior subjective synonym of Astarte carinata (Phillips, 1829), of which a holotype was refigured by Duff (1978, pl. 11, fig. 13), from the Oxford Clay of Yorkshire.

Diagnosis (emended). Small nicaniellid, trigonal in outline with very prominent swollen umbones. Posterodorsal margin concave. Dental formula as given for genus, but with 3a obscured by lunule development and 6b not seen.

Remarks. See discussion of N. (Nicaniella).

Nicaniella (Trautscholdia) claxbiensis (Woods, 1906) Pl. 27, figs 20–29; Text-fig. 73B

- *v. 1906 Astarte claxbiensis sp. nov. Woods, pp. 108–109, pl. 14, figs 25–28. [Spilsby Sandstone and Claxby Ironstone of Lincolnshire].
- p. 1924b Astarte claxbiensis Woods; Gillet, p. 102 [Claxby Ironstone only; non pl. 2, fig. 6, Albian of Morocco = Nicaniella (Nicaniella) sp.].
 - 1977 Astarte claxbiensis Woods; Pyrah, p. 247 [Syntype, Neocomian, Benniworth Haven, Lincolnshire].
 - 1979 Nicaniella claxbiensis (Woods); Gallois & Morter, p. 30 [Mintlyn Beds, Ryazanian, The Wash borehole 72/77B].
- v. 1983 Nicaniella (Trautscholdia) claxbiensis (Woods); Kelly & Rawson, p. 69 [Claxby Ironstone, Benniworth Haven, Lincolnshire].

Type specimens. Woods (1906) listed at least five syntypes preserved in the Sedgwick Museum, Cambridge, including (SMC B.11355,11356), and the Yorkshire Museum (YM 918), which came from the Claxby Ironstone of Benniworth Haven. The specimen from the Spilsby Sandstone of Spilsby, (SMC B.11354) which was figured by Woods (1906, pl. 14, fig. 25a-c), is designated here as lectotype. Wood's figure is twice natural size. The specimen is refigured here (Pl. 27, fig. 28). The age of the Claxby Ironstone specimens is probably Lower Valanginian; the precise age of the Spilsby Sandstone specimen is uncertain.

Material. 30 specimens. Three specimens, Basal Spilsby Nodule Bed, Middle Volgian, locality 3, Nettleton, Lincolnshire. Two specimens associated with *Paracraspedites* in erratic blocks of Lower Spilsby Sandstone, *oppressus* Biozone, Middle Volgian, locality 12, Leziate Sand Pit, Norfolk. Five specimens from bed 1 concretions, Lower Spilsby Sandstone, locality 10, West Keal. 17 specimens BGS Thurrell Collection, Zm2717–2736, Zt3271, Upper Spilsby Sandstone, *albidium* Biozone, Ryazanian, Biscathorpe gravel pit, Louth, Lincolshire; SMC B.12056–12057, Spilsby Sandstone, unspecified horizon, Donington, Lincolnshire; SMC B.12058–12059, Spilsby Sandstone, Spilsby, Lincolnshire.

Diagnosis. Small nicaniellid with prominent swollen umbones; anterior and posterior dorsal margins concave; tooth 3a normally obscured by lunule development.

Description. Shell small with maximum adult length 14 mm and height 14 mm; commissural outline suboval with slightly deeper posterior than anterior; umbones very strongly inflated, constricted and orthogyrate, although degree of inflation of the shell decreases with age; beaks small, weakly prosogyrate and slightly overhanging; posterodorsal and anterodorsal margins concave; anterior margin rounded; ventral margin weakly inflated; posterior margin bluntly rounded; depressed cordate lunule; escutcheon lanceolate; exterior surface ornamented by fine, up to about 25 regular commarginal ribs; hinge and interior as in N. (N.) mnevnikensis differing only by having 3a almost completely obscured by lunule development (Text fig. 73B).

Measurements (In mm, see Text fig. 60).

						denticulate
						or
	Valve	L	Lp	Н	В	smooth
BGS Zm2719	L	9 ∙5	4.5	8∙5	4′	S
Zm2723	R	10	5	9	4·5′	D
Zm2729	L	8∙5	4	8.5	4'	D
Zm2737	L&R	9	4 ·5	8	7.5	D
Zu548	L	12	8	11	5′	S
Zu546/547	R	14	8	15	6′	D
Zu2103/2104	L	11	9	10	_	_
Lectotype: SMC B.11354	L	9+	6	8+	4'	D
B.12057	L&R	9.5	5.5	8	7	D
B .12058	L	9	4.5	8	3.5'	D

TRAUTSCHOLDIA

Discussion. N. (T.) clashiensis differs from N. (T.) cordata (Trautschold, 1860) [= N. (T.) carinata (Phillips)], by having a less constricted umbonal region and more numerous finer ribs on the flank. N. (T.) clashiensis also occurs in the Swindon Clay, the Hartwell Clay (BGS) and in the basal Claxby Ironstone. No specimens have been seen which compare in size with the particularly large specimen illustrated here (Pl. 27, fig. 28) from the Lower Spilsby Member of West Keal.

Occurrence. Middle Volgian of central England; Middle Volgian to early Valanginian of eastern England (Text-fig. 75).



TEXT-FIG. 75. Palaeogeographic distribution of Nicaniella (Trautscholdia) carinata (Phillips) and N. (T.) claxbiensis (Woods)

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PLATES Unless otherwise stated all the figures are reproduced in exterior lateral view and at natural size; specimens were coated with ammonium chloride before photography.

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