SPINUCELLA, A NEW GENUS OF MIOCENE TO PLEISTOCENE MURICID GASTROPODS FROM THE EASTERN ATLANTIC

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The new muricid gastropod genus *Spinucella* is proposed for *Purpura tetragona* J. de C. Sowerby, 1825 (type species), from the Pliocene of the North Sea Basin, and for several other early Miocene to late Pleistocene species from southern Europe, North Africa, and southern Africa. The genus is characterised by the presence of a labral spine on the outer lip of the shell and by reticulate sculpture. Species of *Spinucella* closely resemble members of *Nucella* Röding, 1798, *Acanthina* Fischer von Waldheim, 1807, and *Acanthinucella* Cooke, 1918. The labral spine of *Spinucella* was probably evolved independently of that in the eastern Pacific *Acanthina* and *Acanthinucella*. With the removal of *S. tetragona* from *Nucella*, where many recent authors have placed the species, the time of arrival of *Nucella* in the North Atlantic from the North Pacific was late Pliocene, rather than middle Pliocene.

Key words — *Spinucella*, new genus, *Acanthina*, *Nucella*, Neogene, biogeography.

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INTRODUCTION

The muricid gastropod genus *Nucella* Röding, 1798, comprises eight or nine cool-temperate species found abundantly on rocky intertidal and shallow sublittoral surfaces in the northern oceans. Its type species, *Nucella lapillus* (Linnaeus, 1758) (see Kool & Boss, 1992), occurs on both the European and American sides of the Atlantic, and is the only living representative of the genus in North Atlantic waters. All other species occur in the North Pacific. Several other species have also been assigned to *Nucella*. These include four living and one Pliocene species from South Africa (Kilburn & Rippey, 1982; Kensley & Pether, 1986) and the Pliocene species originally described as *Purpura tetragona* J. de C. Sowerby, 1825, from the North Sea Basin of western Europe (see Harmer, 1914-1921; van Regteren Altena *et al.*,

1956; Glibert, 1959, 1963). In fact, Glibert (1959) considered *N. tetragona* to be ancestral to *N. lapillus*, the two species being linked by the late Pliocene taxon *N. lapillus incrassatus* (J. de C. Sowerby, 1825). According to this interpretation, *N. tetragona* would be the earliest species of the genus in the North Atlantic, and invasion of *Nucella* from the Pacific, where *Nucella* can be traced back to the early Miocene, would have taken place no later than middle Pliocene time (Crothers, 1983; Vermeij, 1991).

Authors who regard *Purpura tetragona* as a species of *Nucella* have overlooked several characters that distinguish this species from all other members of that genus. In our study of the phylogeny of *Nucella* (Collins *et al.*, in prep.), we found that *P. tetragona* possesses a small but distinct labral spine, a ventral projection at the anterior end of the outer lip of the shell. This feature is characteristic of *Acanthina* Fischer von Waldheim, 1807. Lecointre (1952), who considered *Acanthina* to be a subgenus of *Nucella* (or *Purpura* in his terminology), assigned *P. tetragona*, along with several other Pliocene and Pleistocene species from Morocco and southern Europe, to *Acanthina* [type species: *A. monodon* (Pallas, 1774)]. One of the species from Morocco was considered by Lecointre (1952) to be specifically indistinguishable

from *A. monodon unicornis* (Bruguière, 1789) (*A. crassilabrum* Lamarck in Lecointre's terminology), from southern South America.

A re-examination of *Purpura tetragona* and of various other species assigned to *Nucella, Acanthina*, and related groups indicates the existence of an early Miocene to late Pleistocene lineage of eastern Atlantic muricids possessing a labral spine and reticulate sculpture. The purpose of this paper is to recognise and name this lineage as the new genus *Spinucella*, with *Purpura tetragona* as type, and to discuss the characters, evolution, and biogeographical relationships of this group and morphologically similar muricids.

SYSTEMATICS

Family	Muricidae Rafinesque, 1815
Subfamily	Ocinebrinae Cossmann, 1903
Genus	*Spinucella* nov. gen.

Type species — *Purpura tetragona* J. de C. Sowerby, 1825, here designated.

Diagnosis — Shell ovate; spire shorter than adult body whorl; teleoconch whorls four to five in number, evenly rounded or slightly shouldered; sculpture of both spiral and axial elements; spiral ribs usually broad, up to seven primaries on body whorl, with intercalated secondary ribs and finer threads; axial ribs form a reticulate or latticed pattern with the spiral sculpture; aperture ovate; junction of outer lip with body whorl continuous, without posterior sinus or notch; edge of outer lip at base of siphonal canal with short labral spine, formed as an elaboration of one of the denticles on the inner surface of the outer lip; outer lip slightly thickened, denticulate within, the denticles developed close to the edge of the lip; columella more or less straight, sometimes flattened, lacking folds; siphonal canal open, its trace visible on the shell's exterior as a prominent fasciole often separated from the base by a pseudo-umbilical slit.

Geographical and stratigraphical distribution — Early Miocene to late Pleistocene; North Sea Basin to southern Africa.

Included species — The type of *Spinucella* is *S. tetragona* (J. de C. Sowerby, 1825), which has been recorded in England from the Coralline Crag at Ramsholt and from throughout the Red Crag (Waltonian, Newbournian, and Butleyan) (see Harmer, 1914-1921; Glibert, 1963). In Belgium the species is known from the Oorderen Sands Member of the Lillo Formation (Glibert, 1958, 1959). In The

Netherlands, *S. tetragona* is found washed up on beaches in the estuary of the Westerschelde in the province of Zeeland (van Regteren Altena et al., 1956). It therefore has a geological range of middle to late Pliocene.

The shell of *Spinucella tetragona* is moderately large (up to 63 mm in length), characterised by a relatively high spire, long siphonal canal, well-marked pseudo-umbilical slit, a rounded columella, a deep suture, a very short labral spine, and strong latticed sculpture consisting of six major spiral cords crossed by as many as fifteen axial folds (Pl. 1).

A second well-characterised species is *S. plessisi* (Lecointre, 1952) from the late Pliocene to late Pleistocene of the warm-temperate eastern Atlantic (Pl. 1, Fig. 5). This species had a range from near Lisbon (Portugal) to Morocco and the Canary Islands; a single (presumably fossil) specimen has been collected in sediment near Cape Bojador, Spanish Sahara (see Brébion, 1974, 1979a, b; Meco, 1981). *Spinucella plessisi* is rather variable in shape and in the development of shell sculpture. Almost smooth forms were called *Purpura (Acanthina) crassilabrum* Lam. by Lecointre (1952). More heavily sculptured forms with a reticulate sculpture of spiral and axial ribs were named *P. (A.) plessisi, P. nicklesi*, and *P. nicklesi* var. *imsouanensis*, all of Lecointre (1952). Brébion (1974, 1979a, b) and Meco (1981) justifiably synonymised all these forms under the earliest available name, *P. (A.) plessisi* Lecointre, 1952, which is here placed in *Spinucella*. *S. plessisi* differs from *S. tetragona* by the absence of a pseudo-umbilical slit, by having a lower spire, and by having the suture indistinct rather than deeply impressed.

Perhaps the earliest representative of *Spinucella* is *S. angulata* (Dujardin, 1837) from the middle Miocene (Helvetian = Tortonian) of France. This species differs from most other members of the genus by its small size (length of adults up to 34 mm) and by its sculpture of six to seven very thick axial ribs, which form nodes where they are crossed by five or six closely spaced spiral cords. The uppermost spiral cord forms a weak shoulder, above which the straight axial ribs slope towards the indistinct suture.

Several other southern European species from the Miocene and Pliocene appear to belong to *Spinucella*. These include *S. monacanthos* (Brocchi, 1814) from the Pliocene of Italy, *S. depressa* (Bronn, 1831) from the Pliocene of Italy, *S. cancellata* (Bellardi, 1882) from the early and late Miocene of Italy, *S.*

benoisti (Degrange-Touzin, 1895) from the Helvetian of France, and *S. lesvignesi* (Cossmann & Peyrot, 1923) from the Tortonian of France. It is doubtful that all these names refer to distinct species, but I have not undertaken a critical review of these taxa.

Another species that appears to belong to *Spinucella* is the Pliocene South African *S. praecingulata* (Haughton, 1932), described from the west coast of Cape Province. This large species, which reaches a length of 115 mm, is highly variable in spire height and in the development of shell sculpture. As Kensley & Pether (1986) pointed out, low-spired shells are typically strongly sculptured, whereas higher-spired shells are less heavily ornamented. On shells with well-developed sculpture (Pl. 1, Figs 1, 2), there are seven primary spiral ribs on the body whorl (three on the penultimate whorl), forming a network sculpture with subsidiary axial folds visible in the interstices between the spiral elements. The axial sculpture is often missing in later whorls, but is usually present on early whorls. There is a trace of a labral spine in one of the specimens that I have been able to examine, courtesy of J. Pether at the South African Museum (Pl. 1, Figs 1, 2). In specimens whose outer lip is thickened within, the denticles are close to the edge of the outer lip. There is typically no pseudo-umbilical slit. The reticulate sculpture, obsolete but recognisable labral spine, and the character of the outer lip dentition are all strongly reminiscent of *S. tetragona*. The two species differ in that *S. praecingulata* is larger (up to 115 mm as compared to 63 mm), lacks a slit-like pseudo-umbilicus, has a weaker labral spine, and has reduced axial sculpture. Differences between *S. praecingulata* and the other South African species typically referred to *Nucella* will be treated below.

COMPARISONS

It is easy to understand why *Spinucella tetragona* has long been regarded as a species of *Nucella*. *Spinucella* and *Nucella* are similar in shell shape, in the absence of columellar folds, in the absence of a posterior notch or sinus, and the presence of denticles on the inner surface of the outer lip. The diagnostic labral spine of *S. tetragona* is often invisible because the anterior part of the outer lip is frequently corroded or damaged in fossil shells.

Spinucella differs from *Nucella* in three shell characters. First, it possesses a labral spine, whereas *Nucella* does not. Secondly, the denticles on the inner surface of the outer lip lie close to the edge of the lip in *Spinucella*, whereas in *Nucella* they are deeply recessed. The inner surface of the outer lip of *Nucella* is thus bevelled, whereas in *Spinucella* it is not. In the third place, the lattice-like sculpture characteristic of *Spinucella* does not occur in *Nucella*. In species of *Nucella* with axial elements, the latter are either discrete knobs, as in some thick-shelled morphs of *N. emarginata* (Deshayes, 1839) from California, or they are irregularly spaced flanges that override the spiral cords, as in the northeastern Pacific *N. lamellosa* (Gmelin, 1791) and the northwestern Pacific *N. heyseana* (Dunker, 1882).

The four living South African species that have been assigned to *Nucella* by previous authors comprise a heterogeneous group differing in shell sculpture and egg-capsule characters from northern hemisphere members of *Nucella* (see also d'Asaro, 1991; Vermeij, 1992) as well as from species of *Spinucella*. *'Nucella' squamosa* (Lamarck, 1816) and *'N.' dubia* (Krauss, 1848) differ from both genera in possessing a slight thickening on the inner lip adjacent to the junction of the outer lip with the body whorl. Moreover, *'N.' squamosa* has a slight notch or sinus at the posterior end of the outer lip. Many specimens of *'N.' squamosa* have regularly spaced thin axial folds that cross eleven to seventeen spiral cords on the body whorl to form a relatively fine cancellate sculpture. The axials tend to override the spirals, whereas in sculptured specimens of *Spinucella* the spiral elements tend to be dominant. *'Nucella' dubia* has irregular weak spiral cords and lacks well-defined axial sculpture. *'Nucella' cingulata* (Linnaeus, 1758), type species of *Trochia* Swainson, 1840, has up to five broad, prominent, almost T-shaped spiral cords, but again lacks axial sculpture. This species, as well as *'N.' dubia* and *'N.' squamosa*, generally has a thin outer lip that is not denticulate within. Finally, *'N.' wahlbergi* (Krauss, 1848) differs greatly from all other species discussed here in having a high spire, a long, almost closed siphonal canal, and a sculpture of numerous fine axial and spiral lines. There is a distinct posterior thickening on the inner lip at the posterior end of the aperture, as in *'N.' squamosa*. The ventral portion of the body whorl of *'N.' wahlbergi* projects ventrally beyond the plane of the aperture. A labral spine is absent in all four living South African species of *'Nucella'*.

Lecointre (1952) and Brébion (1974) assigned species of *Spinucella* to the genus or subgenus *Acanthina* owing to the presence of a labral spine and to the similarity in overall shell shape to the type species of that group, *A. monodon*. Both genera have a

low spire, a denticulate outer lip, and a smooth, more or less straight columella.

Acanthina differs from *Spinucella* in details of sculpture and in the placement of the labral spine. The living *A. monodon* is a highly variable species that is sometimes divided into a northern subspecies *A. m. unicornis* (Bruguière, 1789) from northern and central Chile, and a southern form, *A. m. monodon* from southern Chile, Tierra del Fuego, and the Falkland Islands (E.H. Vokes, personal communication). In addition, there are various Pliocene forms such as *A. costata* and *A. acuminata*, both of J. de C. Sowerby, 1825 (see Herm, 1969). In the *unicornis* form, the sculpture consists of low smooth spiral cords, which may be obsolete on the body whorl. Their number typically ranges from ten to twenty, but in the Pliocene variety *costata* there are only four to six strong cords. Axial sculpture is absent. In the southern *A. m. monodon*, the spiral cords are often scaly by virtue of the development of thin lamellae on the cords (see also Wu, 1985). The labral spine of the South American species is unique in that it arises from the middle shell layer. In adult as well as in thin-lipped juvenile shells, the edge of the outer lip is sharp and continuous, being slightly creased at the position of the spine but showing no other indication of that projection. The inner edge of the lip also forms a continuous, often finely denticulate, ledge. Between this inner ledge and the sharp outer edge of the lip, the labral spine arises from a bevelled surface in the middle of the wall of the outer lip. In *Spinucella*, by contrast, the labral spine arises from both the outer and inner shell layers, and is therefore a ventral projection of the lip as a whole rather than only of the middle layer.

In the position of the labral spine, *Spinucella* resembles several northeastern Pacific species that were assigned by Cooke (1918) to his new taxon *Acanthinucella*, which he regarded as a subgenus of *Acanthina* but which Wu (1985) synonymised with the latter genus. *Acanthinucella punctulata* (G.B. Sowerby, 1835), the type species, has a radula that is essentially identical to that of *Nucella* and somewhat different from that of *Acanthina* s. str. (Cooke, 1918). Species of *Acanthinucella*, which range in age from late Miocene to Recent in California, northwestern Mexico, and Chile, share with *Nucella* the deeply recessed dentition of the outer lip, but they differ from most species of *Nucella* by possessing a small but distinct tubercle on the inner lip at the posterior end of the aperture. This tubercle, which also occurs in some South African species of '*Nucella*'

(see above), is found in some thick-walled individuals of *Nucella emarginata* from California, but is absent in all other species of *Nucella* as well as in *Acanthina* s. str. and in *Spinucella*. The Recent *Acanthinucella spirata* (de Blainville, 1832), *A. punctulata*, and *A. paucilirata* (Stearns, 1872) are characterised by a sculpture of fine spiral threads or riblets and a more or less well-developed shoulder on the body whorl. Axial sculpture is lacking on the body whorl, but does occur as nodes on early teleoconch whorls. A second group of *Acanthinucella*, including *A. lugubris* (J. Sowerby, 1821) from northwestern Mexico and the Pliocene Chilean *A. mirabilis* (Möricke, 1896) and *A. philippii* (Möricke, 1896), has the fine spiral sculpture overridden by thick rounded axial folbs, which form a nodose sculpture. In *A. l. lugubris* and *A. l. angelica* (Oldroyd, 1918), the nodes are arranged in two to four widely separated spiral bands. The axial elements of these species are quite different from the thick rounded axial ribs of *Spinucella*, in which these ribs are overridden by the spiral cords.

As Cooke (1918) and Wu (1985) recognised, '*Acanthina*' *brevidentata* (Wood, 1828) from the tropical eastern Pacific is not a true *Acanthina* but instead is related to *Thais* Röding, 1798 and *Stramonita* Schumacher, 1817. The species differs from *Acanthina* s. str. and from *Spinucella* by possessing a tubercle on the inner lip at the posterior end of the aperture, by having a weak sinus in the outer lip where the latter joins the body whorl, and by having two spiral rows of knobs on the body whorl, as well as by the presence of two weak folds on the columella. The columellar plication and outer-lip sinus set the species apart from the sculpturally similar *Acanthinucella lugubris angelica*.

The distribution of character states among the various taxa discussed above is summarised in Table 1. New supraspecific taxa are warranted for at least some of the living South African species as well as for '*Acanthina*' *brevidentata* from the eastern Pacific, but formal proposals will be deferred until more information on anatomy and reproductive characters becomes available.

EVOLUTIONARY AND BIOGEOGRAPHICAL RELATIONSHIPS

The recognition of *Spinucella* as distinct from *Nucella* has several implications for the interpretation of Neogene historical biogeography. One of these concerns the genus *Nucella*. With *Spinucella tetragona* excluded from *Nucella*, the earliest representative of

Character	Nucella species	"Nucella" squamosa	"Nucella" dubia	"Nucella" cingulata (type of Trochia)	"Nucella" wahlbergi	Acanthina species	Acanthinucella species	"Acanthina" brevidentata	Spinucella species
Inner-lip posterior knob	–*	+	+	–	+	–	+	+	–
Outer-lip posterior notch	–	+	–	–	–	–	–	+	–
Outer-lip dentition	+	–	–	–	–	+	+	+	+
Dentition deeply recessed	+	–	–	–	–	–	+	–	–
Reticulate sculpture	–	+	–	–	–	–	–	–	+
Labral spine	–	–	–	–	–	+	+	+	+
Whole outer lip forms spine	–	–	–	–	–	–	+	+	+
Columellar plaits	–	–	–	–	–	–	–	+	–

Table 1. Presence (+) or absence (-) of shell characters in taxa related to *Nucella*, *Acanthina*, and *Spinucella*. * = present in some individuals of *N. emarginata*.

Nucella in the North Atlantic is the late Pliocene *N. lapillus incrassatus* (J. de C. Sowerby, 1825) from the Merksemian of Belgium and the Red Crag of England (Harmer, 1914-1921; Glibert, 1958, 1959, 1963; Cambridge & Kitching, 1982). That this form is a true *Nucella* is indicated by the absence of axial sculpture and of a labral spine, as well as by the distinctly bevelled outer lip. The invasion of *Nucella* from the North Pacific via the Bering Strait to the North Atlantic may therefore have occurred later (during late Pliocene time) than had been supposed by Durham & MacNeil (1967) and Vermeij (1991), who indicated a mid-Pliocene date.

It could be argued that the stock of *Nucella lapillus* in the Atlantic is derived from *Spinucella* by loss of the labral spine, and that *N. lapillus* is not the descendant of a North Pacific invader at all. Molecular data (Collins *et al.*, in prep.) as well as far-reaching similarities between *N. lapillus* and Pacific species of *Nucella* cast doubt on this hypothesis.

An interesting question is how *Acanthina* and *Spinucella* are evolutionarily related. French authors have generally referred European and North African *Nucella*-like gastropods with a labral spine to the genus or subgenus *Acanthina*, and in doing so have implicitly or explicitly inferred a close phylogenetic connection with South American representatives of that group (Lecointre, 1952; Brébion, 1974). The alternative interpretation is that labral spines were evolved independently by *Acanthina* in the eastern Pacific and by *Spinucella* in the eastern Atlantic.

Support for the interpretation that a direct phylogenetic connection exists between *Acanthina* and *Spinucella* would come from evidence that other lineages also occurred in both the eastern Pacific and eastern Atlantic. Two gastropod genera satisfy this criterion. One of these is the limpet-like muricid genus *Concholepas* Bruguière 1792. During the middle Miocene, this genus (or a group very closely related to it) is known from France, Florida, Australia, and New Zealand (Beu, 1970; Vokes, 1972a). From Pliocene to Recent time, *Concholepas* has been essentially confined to the temperate west coast of South America (Herm, 1969), although Kensley (1985) reported one late Pleistocene find on the west coast of South Africa. The calyptraeid genus *Trochita* Schumacher, 1817, is known from the Pliocene to middle Pleistocene of Morocco and the Canary Islands (Brébion, 1979b; Meco, 1981) and in the Miocene and Pliocene from tropical America (Vokes, 1975). Today the genus occurs sporadically in the Cape Verde Islands, Angola, southern Africa, the Gulf of Oman, New Zealand, southern South America, and from Mexico to Chile in the eastern Pacific (Taylor & Smythe, 1985). Like *Spinucella*, *Trochita* became extinct on the mainland coast of

North Africa during the late Pleistocene. Many tropical genera are known to have discontinuous modern distributions, with species in the eastern Atlantic and eastern Pacific but not the intervening western Atlantic. Examples include the gastropods *Harpa* Röding, 1798, *Pseudozonaria* Schilder, 1927, *Erosaria* Troschel, 1863, *Purpurellus* Jousseaume, 1880, and *Sveltia* Jousseaume, 1887 (see Rehder, 1973; Vokes, 1984, 1989; Vermeij, 1986; Jung & Petit, 1990). Western Atlantic representatives of these genera are known only from the Miocene or Pliocene. If *Acanthina* and *Spinucella* have a common ancestor possessing a labral spine, they would constitute a single lineage that should conform to the biogeographical history of the genera discussed above. In other words, there should be a *Nucella*-like species with a labral spine in the Miocene or Pliocene of the western Atlantic. To date, no such candidate species has yet been found in the very rich fossil record on the Atlantic coasts of North and South America.

I am inclined to think that *Acanthina* and *Acanthinucella* in the Pacific evolved labral spines independently of the eastern Atlantic *Spinucella*. The difference in spine formation and in shell sculpture between Pacific and Atlantic forms (see Table 1) indicates convergence rather than common descent. Cooke's (1918) finding that the radula of the northeastern Pacific *Acanthinucella* is virtually identical to that of *Nucella* points to a close phylogenetic affinity between these genera, both of which date from the Miocene in the North Pacific. The South American *Acanthina* could then have been derived from an intervening stock in the same way that several other South American groups are derived from northern Pacific invaders across the equator (Lindberg, 1991). *Spinucella* may well be related to at least some of the South African species of '*Nucella*'. The latter, in turn, may have a common ancestry with the lineage that also gave rise to *Nucella*. The split between the lineage leading to *Spinucella* and that leading to *Nucella* and *Acanthinucella* would have substantially preceded the evolution of labral spines. According to the anatomical work being carried out by S. Kool (personal communication), *Nucella* belongs in an ocinebrine group together with several southern hemisphere genera that, based on shell characters, could easily accommodate *Spinucella* as well.

This scenario requires that *Spinucella* evolved in the southern hemisphere and subsequently spread northwards to North Africa and Europe. Although a pre-Pliocene record of *Spinucella* is unknown in southern or in tropical West Africa, the genus does conform to a biogeographical pattern that is seen in several other temperate genera. As documented by Vermeij (1992), a biogeographical connection between the northern and southern temperate zones in the eastern Atlantic had been established by Pliocene time. It will be interesting to see if other extinct elements of the North Sea Basin biota of the Miocene and Pliocene can be linked with species from the temperate southern hemisphere. Maxwell's (1988) interpretation that the middle Miocene North Sea Basin turrid *Magnella dittmeri* Anderson, 1960, represents a species of the New Zealand genus *Mioawateria* Vella, 1954, is consistent with a link between northern and southern temperate faunas in the Old World during the Miocene. So is the distribution of *Pterynopsis* Vokes, 1972, an Oligocene to late Pliocene genus of muricids known from both the North Sea Basin and Namibia (Vokes, 1972b). Future worldwide revisions of groups will be needed to uncover and document patterns such as these.

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PLATE 1

Figs 1, 2.   *Spinucella praecingulata* (Haughton, 1932), Hondeklip, South Africa. Dorsal (Fig. 1) and apertural (Fig. 2) views. Collections of the South African Museum, SAMPQHB 136, x 1,4.

Figs 3, 4.   *Spinucella tetragona* (J. de C. Sowerby, 1825), Ellewoutsdijk, province of Zeeland, The Netherlands. The small labral spine (Fig. 3) is clearly visible despite slight damage to the outer lip. Collections Nationaal Natuurhistorisch Museum, Leiden, ST 101186, x 2.5 and 4.1, respectively.

Fig. 5.   *Spinucella plessisi* (Lecointre, 1852), Sidi Bou Maleh, Morocco. Collections of the Academy of Natural Sciences, Philadelphia, ANSP 77360, x 2.5.

PLATE 1