Smeagolida, a new order of gymnomorph mollusc from New Zealand based on a new genus and species

F. M. Climo

National Museum of New Zealand, Private Bag, Wellington, New Zealand

Smeagol manneringi n.gen. & sp. is erected as the only known representative of a new order, Smeagolida, and is compared with existing gymnomorph orders. The relative ranking of Gymnomorpha, Opisthobranchia, and Pulmonata is discussed, and use of the name Systellommatophora is abandoned. The gymnomorph slugs are interpreted as a polyphyletic assemblage of stem euthyneurans, but subclass Gymnomorpha is retained as a convenient grouping.

Keywords: Mollusca; Gymnomorpha; Smeagolida new order; *Smeagol manneringi* new genus and species; taxonomy; classification; interstitial habitat

INTRODUCTION

In 1971 Mr I. Mannering discovered some peculiar slugs on the Kaikoura Peninsula. Their puzzling external features and interstitial habitat high in the intertidal limestone gravels led Mannering to examine them in more detail.

In 1973 he confided in me regarding his discovery and provided some rough sketches showing the general layout of body organs. His collection of specimens was sent to me when his career interests subsequently diverged from marine biological research. Mr Mannering made it known to several persons between 1971 and 1973 that he felt he had discovered a new order of mollusc, but his conclusion was not developed to the point of publication.

My formative ideas on the classification of Mannering's slug, which is described here, were presented in a paper delivered at the International Molluscan Symposium at the Australian Museum, Sydney, in May 1979. Since then, several drafts of the manuscript have been circulated among malacologists with opisthobranch research leanings, for critical comment. The ideas finally expressed here were shaped by the above correspondence and by discussions with my New Zealand colleagues, but I take full responsibility for them.

My original dissections were of material collected by Mannering in 1971, and his sketches were used as a guide. Subsequent dissections and serial sections were made from specimens collected at Kaikoura Peninsula by Mr J. van Berkel (Edward Percival Field Station, Kaikoura) in December 1976. Live material examined was collected by Mr B.A. Marshall (National Museum of New Zealand) from the Kaikoura Peninsula and by myself from Wellington gravel shores in December 1979.

Longitudinal and transverse 10 μm serial sections were made of the slug, stained with Delafield's haematoxylin, and counterstained with eosin. The information so obtained confirmed structural interpretations based on macrodissection techniques.

HIGHER CLASSIFICATION – A PREAMBLE

Literature debating the opisthobranch *versus* pulmonate features of the families Onchidiidae, Veronicellidae, Rathousiidae, and (by European workers) Rhodopidae—the so-called gymnomorph (Salvini-Plawen 1970) or systellommatophoran (Solem 1978) slugs—is scattered, and complicated by phylogenetic significance being placed on different organ systems by different authors. Solem (1978) summarised these arguments based on conclusions and new evidence (or ideas) provided by Fretter (1943), Pilsbry (1948), Baker (1955), Boettger (1955), Solem (1959), Stringer (1963), Ghiselin (1966), Van Mol (1967), Peterellis & Dundee (1969), Oberzeller (1970), Salvini-Plawen (1970), and Minichev & Slavoshevskaya (1971). The development of ideas is continued by Minichev (1975), Minichev & Starobogatov (1975), and Salvini-Plawen (1979).

The present consensus seems to be something of a compromise, the three or four families (depending on whether Rhodopidae is included) being treated as a separate, monophyletic lineage with pulmonate and opisthobranch features. The level at which they are classified as different seems as variable as the opinions of authors, but a basic dichotomy is evident. Solem (1978), stressing the evidence of Pilsbry (1948), Baker (1955), Ghiselin (1966), and Van Mol (1967), treated these slugs as a superorder in subclass Pulmonata, whereas Salvini-Plawen (1970,

Received 18 July 1980

1979) stressed his own findings, supported by the conclusions of Fretter (1943) and Boettger (1955), and treated the gymnomorphs as a separate subclass equal in rank to Opisthobranchia and Pulmonata.

Expressed in a formal way, the two systems of classification appear as follows. That followed by Solem (1978, 1979):

Subclass PULMONATA
  Superorder SYSTELLOMMATOPHORA
    Order ONCHIDIACEA
      Family Onchidiidae
    Order SOLEOLIFERA
      Family Veronicellidae
      Family Rathousiidae
  Superorder STYLOMMATOPHORA
  Superorder BASOMMATOPHORA

That followed by Salvini-Plawen (1970, 1979), with ordinal name endings in the convention of Minichev (1975):

Subclass OPISTHOBRANCHIA
Subclass PULMONATA
Subclass OPISTHOPNEUMONA Minichev, 1975
  (=GYMNOMORPHA Salvini-Plawen, 1970)
    Order ONCHIDIIDA
      Family Onchidiidae
    Order RATHOUSIIDA
      Family Rathousiidae
      Family Veronicellidae
    Order RHODOPIDA
      Family Rhodopidae

Strict rules of priority do not apply to names for categories at the ordinal and subclass levels, a degree of flexibility that is causing nomenclatural chaos in this area of gastropod classification.

An historical summary of the taxonomic nomenclature of gymnomorphs is provided by Forcart (1953, p. 24).

From information provided by the above literature it might seem logical to conclude that the gymnomorph/systellommatophoran slugs had their phylogenetic roots somewhere near the opisthobranch–pulmonate dichotomy, assuming (as suggested by Fretter (1943)) a common ancestry for those subclasses. If valid, this hypothesis would explain the combination of so-called pulmonate and opisthobranch features shared by all gymnomorph slugs.

Rudman (1970) has presented the most comprehensive review of arguments covering the pulmonate *versus* opisthobranch origins of families Onchidiidae, Veronicellidae, and Rathousiidae. His analysis centres on the opposing views of Ghiselin (1966) and Fretter (1943), though other relevant literature up to 1969 is covered also. Rudman considers that the androdiaulic reproductive system of members of the Onchidiidae and Veronicellidae tips the balance towards their being more pulmonate than opisthobranch—". . . it is a pulmonate tendency to develop an androdiaulic system and to develop an internal vas deferens".

To my knowledge nobody has disproved Fretter's contention that the lung of *Onchidella* is not homologous with that of the Pulmonata. Rudman sums that situation up with a convenient dismissal: "While, without embryological evidence, it is difficult to dispute her contention, it is equally difficult for her to sustain it"; and there the matter rests.

Rudman feels that the Onchidiidae are ". . . exhibiting a stage in the colonisation of the land from the sea" and that the Veronicellidae ". . . represent a terrestrial form of a third and distinct group of the Pulmonata, the order Soleolifera", with respect to these families supporting the Ghiselin–Solem system of classification.

Correspondence with Rudman (February 1980) indicates that it might be better to treat the gymnomorph slugs as neither pulmonate nor opisthobranch. The argument developed is that *if* euthyneuran gastropods are monophyletic and arose by explosive radiation we must expect to find small 'minor' groups in the radiation that are taxonomically equal in rank to the more obvious end-product groups exemplified by Opisthobranchia and Pulmonata. Adopting this probably realistic approach would negate much of the tangled debate centred around opisthobranch *versus* pulmonate features of, particularly, the Onchidiidae. The erection of a separate subclass for the Rhodopidae, Veronicellidae, Rathousiidae, and Onchidiidae by Salvini-Plawen (1970 – Gymnomorpha) and Minichev (1975 – Opisthopneumona) seems to have considerable merit.

I follow the Salvini-Plawen–Minichev system of higher classification in placing the enigmatic New Zealand slug described below, but make no attempt to assess relative rankings within the Gymnomorpha. Further, it has not been possible to resolve the debate as to whether the onchidiid lung is homologous with the pulmonate lung. That the lung of the slug described below is homologous with that in an onchidiid slug seems beyond question, however.

As Table 1 shows, the nominal orders of the Gymnomorpha are morphologically quite diverse. On the basis of the Salvini-Plawen–Minichev classification the slug described below belongs in a new order. Its morphological features together strain to the extreme the rather tight concept of Gymnomorpha envisaged by Salvini-Plawen (1970), particularly the androdiaulic reproductive apparatus combined with a syntremous condition. Salvini-Plawen (pers. comm.) is of the opinion that it is a pulmonate, but that interpretation fails to resolve its apparent lung-homology with *Onchidella*.

SYSTEMATICS AND DESCRIPTION

Subclass GYMNOMORPHA

SMEAGOLIDA new order

A monotypic taxon based on the morphology of *Smeagol manneringi* n.gen. & sp., described below, and compared in Table 1 on definitive characteristics with the three existing gymnomorph orders. Characteristics of Smeagolida are as follows.

(1) Animal very active (locomotion by muscles, not cilia), without tentacles, unpigmented, blind, high intertidal, interstitial, up to 10 mm long.
(2) Foot modified into a sucker in region of anterior pedal mucus gland.
(3) Mantle cavity opening dorsally at posterior extremity and supplied with:
   (a) hindgut, on the left;
   (b) a pallial gland (?) modified for respiration, central left;
   (c) a renal papilla, far left.
(4) Visceral ganglion displaced to the right.
(5) Diaulic-syntremous reproductive system opening on right side between head and pedal mucus gland complex.
(6) Nidimental complex composed of a single-lobed posterior albumen gland and two anterior mucus glands.
(7) Prostatic tissue concentrated at distal end of vas deferens.
(8) Penis pierced by vas deferens and enclosed in a sheath.
(9) Salivary glands fused posteriorly below oesophagus.
(10) Stomach divided into a thin-walled anterior and a thick-walled posterior section, with a single opening to digestive gland in between.

SMEAGOLIDAE new family

The characteristics of the family are the same as those listed above for the order.

Smeagol new genus

TYPE-SPECIES (here designated): *Smeagol manneringi* n.sp.

The characteristics of the genus are the same as those listed above for the order and described in more detail below for the type-species.

ETYMOLOGY. The genus takes its name from the pallid, sometimes subterranean Tolkien character Smeagol (whose alternative name is Gollum), a pitiable humanoid who ultimately played a very important role in saving 'Middle Earth' from evil forces. The slug described below is far more significant, phylogenetically, than its drab exterior indicates—hence the analogy. Gender masculine.

Table 1. Select list of morphological features of the Gymnomorpha, showing character-state correlations at family level; plus comparison of habitats

Character	Onchidiidae	Veronicellidae	Rathousiidae	Rhodopidae	Smeagolidae
Cuticularised notum	yes	yes	yes	no	yes
Soleolae on foot	no	yes	yes	no	no
Pallial area	right to terminal	terminal	right	right	terminal
Female gonopore	posterior	right	right	right	anterior
Pneumostome	separate to mantle	absent	separate to ureter/rectum	absent	=mantle opening
Genital apparatus	diaul-diatremous	diaul-diatremous	diaul-diatremous	monaulic	diaul-syntremous
Bursa copulatrix	present	absent	present	absent	present
Albumen gland	paired	single	single	single	single
Jaw	circular	goniognath	absent	absent	absent
Radula	unicuspid-tricuspid	unicupsid	unicuspid	absent	unicuspid
Digestive gland	3 lobes 3 ducts to stomach	multilobed	1 lobe 1 duct to stomach	1 lobe 1 duct to stomach	1 lobe 1 duct to stomach
Visceral ganglion	left	left	left	left	right
Lung	yes	no	not clear from literature	no	yes
Habitat	intertidal to terrestrial	terrestrial	terrestrial	intertidal	intertidal

Smeagol manneringi n.sp. (Fig. 1-3)

EXTERNAL FEATURES. A small slug approximately 1 cm long when crawling actively. Opaque white; darker-coloured digestive gland and ovotestis show through semitransparent dorsal integument. Very active, able to crawl in a gliding motion by means of regular muscular waves passing along foot; strongly negatively phototactic. In life (Fig. 1C-E) shape variable; when crawling on a flat surface similar in shape to a terrestrial arionid slug; can also contract into a short, domed form resembling a resting onchidiid slug; when squeezing through confined spaces appears similar to a triclad platyhelminth.

In preservative (Fig. 1A) animal thickest in posterior third, tapering gently towards head region then more steeply to the blunt anterior extremity. Posteriorly, body outline curves evenly and steeply from thickest point above ovotestis.

Upper surface covered by an integument (notum: mantle) forming a flap peripherally (hyponotum) and defined ventrally by a nearly continuous peripodial groove. Peripheral flap continues round head after an indentation at anterior end of foot. Mantle flaps on head expandable into a pair of lappets, giving a triclad appearance to anterior end when these sensory organs are expanded (Fig. 1E). Posterior four-fifths of foot with a smooth surface, capable of rhythmic muscular waves (in locomotion) or local contractions, dorsally, the latter forming partial-vacuum attachment areas by peripheral adhesion of hyponotum and adjacent parts of sole.

Anterior fifth (same qualifications as above) of foot modified into a sucker, demarcated from rest of foot by a deep, transverse pedal groove and from poorly defined head by a shallow groove. Sucker composed of structures surrounding pedal mucus gland; foot in this region resembles a low mushroom with mucus gland in the stalk. Velum of this structure overhangs further posteriorly than anteriorly and has two posteriorly directed lateral projections. A deep, anteriorly directed recess under central part of velum, posteriorly, narrows anteriorly and communicates with posterior opening of pedal mucus gland (Fig. 1B). This recess, into which the unmodified sole of the foot extends, is the ventral chamber of the pedal mucus gland. The equivalent dorsal (anterior) chamber is not well developed, and only a small pore (anterior opening to pedal mucus gland) opens in this neck region, which is not greatly recessed posteriorly.

Dorsal surface of slug lined by a cuticularised pallisade epithelium, the cuticle raised into microvilli. Abundant subepithelial globular cells (mainly mucocytes) extend canals to surface that open as pores, giving surface a cratered appearance.

Sole of foot (and surface of velum over pedal mucus gland) ciliated, the cilia distributed as tufts on epithelial cells; sole also cratered by mucocyte pores. Peripodal groove ciliated in a similar way to sole of foot, but without mucocyte pores.

Ventral surface of hyponotum histologically similar to sole of foot, but epithelium more heavily cuticularised and clumps of cilia on epithelial cells welded into spikes. Spikes probably play anchoring role in locomotion when hyponotal flap rhythmically raised and lowered in phase with muscular pulses along foot.

Ventral surface of head raised into longitudinal microscopic ridges covered by a pallisade of very narrow, elongate cells that send small spikes to surface through a very thin cuticle. These cells overlie a complex subepithelial layer of muscle fibres and nerves, and are probably sensory in function. There are no tentacles or eyes. Mouth centrally placed on broad, flattened undersurface of head.

Mantle cavity opens as a dorsoventral slit on dorsal midline at posterior extremity. Hermaphroditic gonopore opens on right side in peripodial groove of neck.

ALIMENTARY CANAL. Mouth opening on underside of broad, ill defined, flat-based head, surrounded by lip-like folds; there are no jaws. Buccal mass large, muscular, with oesophagus emerging in anterodorsal third; odontophore projecting posteriorly on right side of oesophagus. A pair of salivary glands enter buccal mass on either side of junction with oesophagus, run posteriorly through nerve ring, then curve under oesophagus and fuse; glands ropelike, of uniform thickness throughout their length.

Oesophagus ascends dorsally after passing through nerve ring, runs caudad to about one-third the length of the animal, then descends to enter stomach on ventral surface of body cavity. Convoluted oesophageal gland lies alongside oesophagus, concentrated mainly to left anterodorsal of nerve ring, then moving progressively ventrad to terminate about level with bursa copulatrix. Gland closely appressed to oesophagus in places, but no connecting duct apparent. Histologically, oesophageal gland appears identical to salivary gland—both composed of a network of angular cells, the contents staining purple.

Oesophagus enters a thin-walled, anterior extension of stomach which passes into a large, heart-shaped region lined by complex folds so oriented as to suggest that it is functionally divided into two sections. Posterior section grades via a small projection into thinner-walled intestine. Single, large digestive gland opens through a duct into thin-walled anterior chamber of stomach, and occupies greater

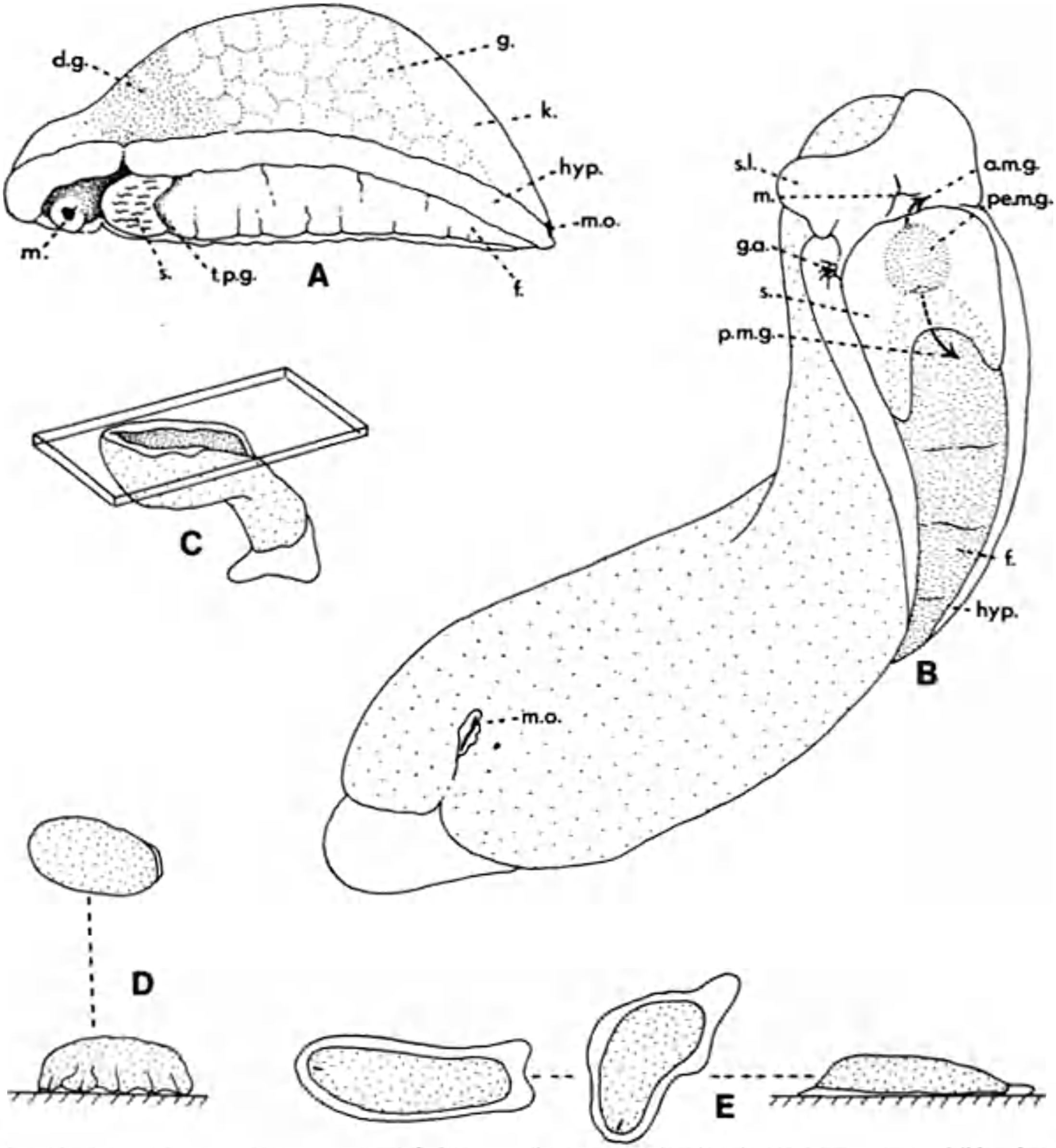

Fig. 1. *Smeagol manneringi*: **A**, external features after preservation in ethanol; **B**, structures visible when live animal is suspended from a slide; **C–E**, body form (dorsal and profile views) when suspended from a slide (C), contracted and immobile (D), and moving (E). Notum lightly stippled.

Legend to Figures

a.g., albumen gland; a.m.g., anterior aperture of pedal mucus gland; ao., aorta; au., auricle; b.c., ursa copulatrix; b.m., buccal mass; cer., cerebral ganglion: d.g., digestive gland; f., foot; g., gonad; g.a., genital aperture; h.g., hindgut; h.d., hermaphroditic duct; hyp., hyponotum; k., kidney; l., lung; m., mouth; m.c., mantle cavity; m.g. 1 & 2, two nidimental mucus glands; m.o., mantle opening; o., odontophore; o.e., oesphagus; p., penis; pap., penile papilla; p. ov., pallial oviduct; ped., pedal ganglion; per., pericardium; p.g., prostatic tissue; p.m.g., posterior aperture of pedal mucus gland; pe. m.g., pedal mucus gland (position of, below sucker); pl., pleural ganglion; p.r.m., penis retractor muscle; p.s., penis sheath; s., sucker; s.g., salivary gland; s.l., sensory lappet; st., stomach; t.p.g., transverse pedal groove; u.p., ureteric pore; v., vagina; v.d., vas deferens; ve., ventricle; visc., visceral ganglion.

part of anterior third of animal. Intestine loops anteriorly over left side of digestive gland (lobes of which partly enfold it in places), plunges ventrally, turns sharply to continue parallel with anterior loop across digestive gland, then extends back as a straight, ciliated tube down left side of animal and opens into mantle cavity. Cross-sections of animal in stomach region consequently show up to 4 intestinal sections (numbers 1–4 in Fig. 3B).

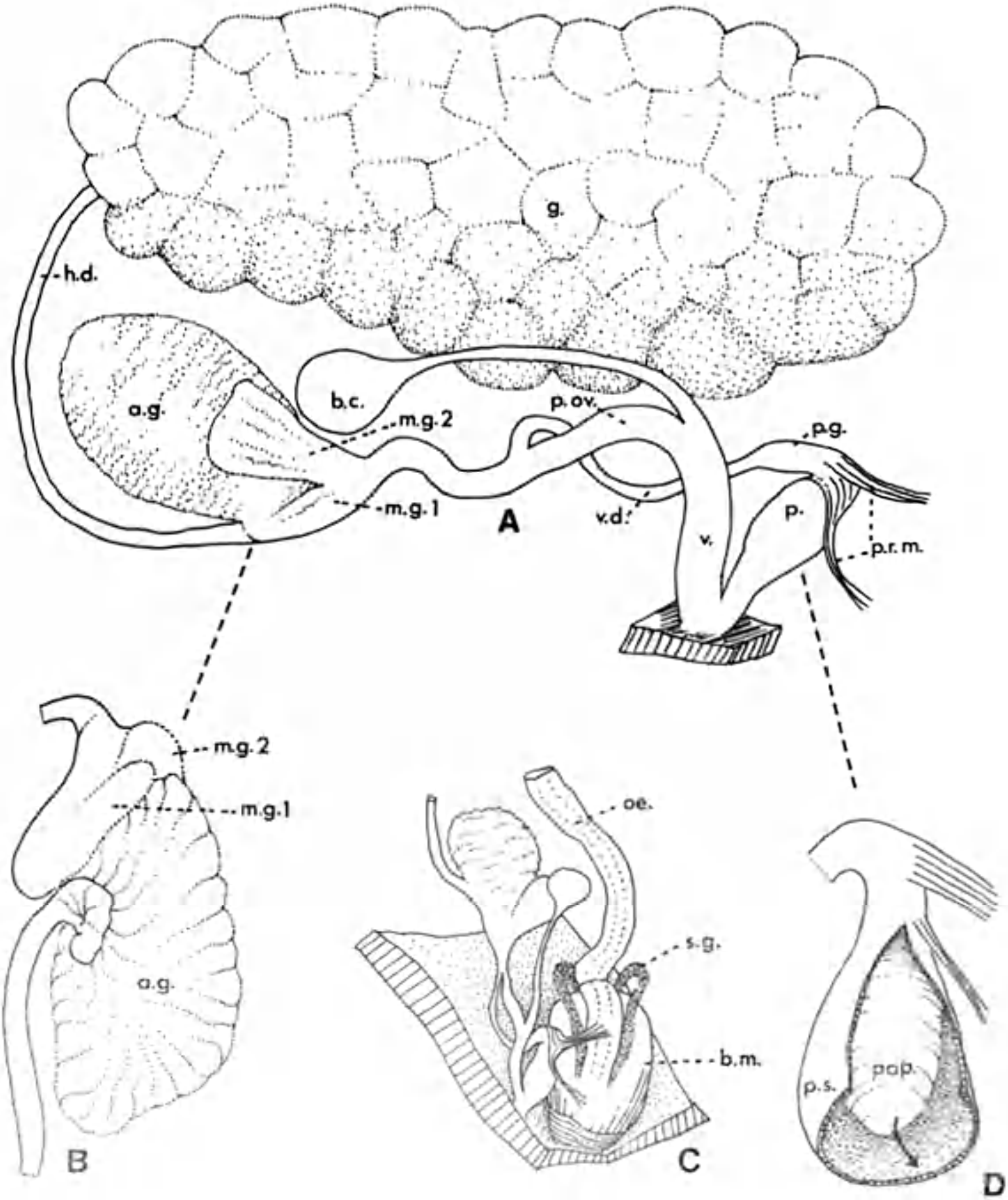

Fig. 2. *Smeagol manneringi*: A, reproductive system; B, opposite side of nidimental complex to that shown in A; C, spatial relationship of reproductive structures to buccal mass; D, penis, dissected.

RADULA. Radular ribbon very wide, only 4–5× longer than wide; 90 rows of teeth present in adults, each with the formula 180–200 + 1 + 180–200. All teeth unicuspid, laterally compressed, in frontal view resembling fence palings; cusped apex occupying about one-fifth of tooth depth. Crown of rachidian set a little lower in cross-row than other teeth; rachidian also identifiable by lack of lateral flexure

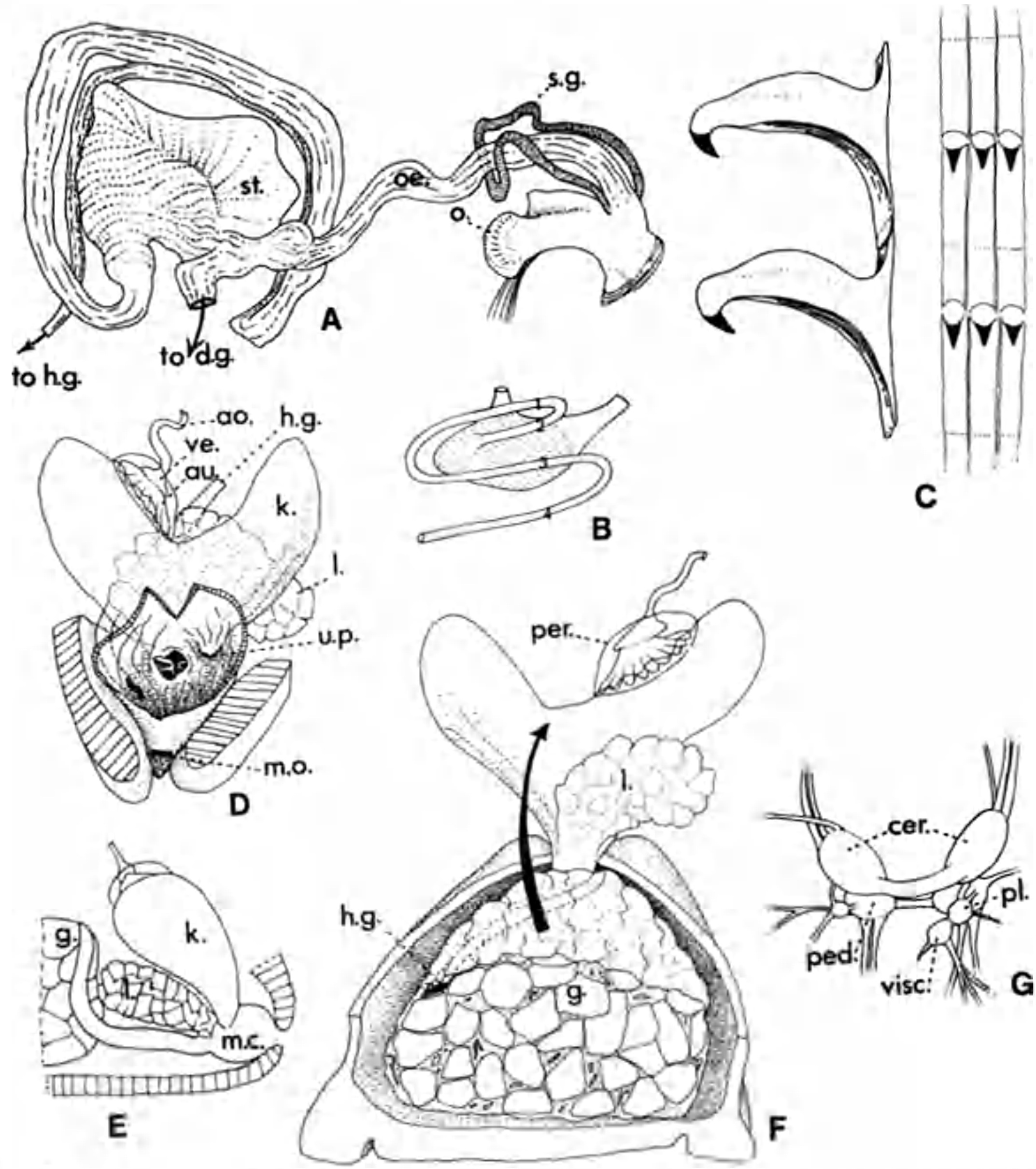

Fig. 3. *Smeagol manneringi*: **A**, alimentary canal (connections to digestive gland and hindgut arrowed); **B**, stomach region (diagrammatic), showing the 4 separate limbs of intestine apparent in transverse sections; **C**, part of radula pallisade, showing 6 teeth in frontal view and 2 in profile (black cutting edges – artistic representation only); **D**, structures at hind end of slug, posterior aspect; **E**, diagrammatic profile of structures shown in D; **F**, structures at posterior end of slug, anterior aspect; **G**, anterior ganglionic complex.

on its basal column. Side views show that a lateral tooth is sickle-shaped and has a projecting posterior buttress and extensive anterior and posterior extensions of the basal plate. Anterior edge of basal plate of one tooth overlaps posterior edge of basal plate of preceding tooth exactly as in the Onchidiidae (Fig. 3C). However, height of each tooth, relative to length of basal plate, much greater in *Smeagol manneringi* than in *Onchidella flavescens*.

REPRODUCTIVE SYSTEM. A diaul-syntremous hermaphroditic system, with single gonopore on right side, in peripodial groove just behind head. All structures anterior to hermaphroditic duct quite small relative to other organs in body cavity, and placed between buccal mass and digestive gland dorsolaterally on right side. Greater part of posterior two-thirds of body cavity occupied by enormous ovotestis composed of 80–90 tightly juxtaposed acini, each angular in fixed material but ovoid in life.

Moving caudad from atrium, reproductive organs arranged as follows (male system first). Penis club-shaped, bulbous in upper third, with vas deferens emerging terminally. Thicker, strongly prostatic distal portion of vas deferens, about one-sixth as long as penis, surrounded at penis/prostate boundary —and partially enveloped—by penis retractor muscle, which comprises 2 branches: larger proximal branch attached to body wall above buccal mass; and smaller, anteriorly directed distal branch extending on to buccal mass at point of entry of oesophagus. Greater part of penis lumen occupied by a simple vergic papilla pierced by vas deferens. Vas deferens, provided with prostatic tissue for its entire length, continues caudad as a simple duct before opening into pallial oviduct.

Vagina a simple duct about as long as penis plus obviously differentiated distal prostate. Main female duct, maintaining same diameter, becomes pallial oviduct at dichotomy with duct of bursa copulatrix. Pallial oviduct between departure of ductus bursae and entry of vas deferens slightly longer than vagina.

Vas deferens and oviduct then fuse externally and pass into nidimental complex. Anterior third of this occupied by 2 mucus glands, a dorsal one staining pale purple and a ventral one dark purple. Dorsal gland composed of oval to hexagonal, closely packed cells with clearly visible walls and randomly distributed nuclei; ventral gland composed of elongate, rectangular cells with indistinct walls and the nuclei grouped at one end. Posterior two-thirds of nidimental complex occupied by strongly surface-folded albumen gland, histologically more dense and staining pinker than mucus glands. Pallial oviduct with lumen large and ciliated as it passes through albumen gland.

Coelomic oviduct is the locally convoluted hermaphroditic duct that passes posterodorsally from albumen gland into ovotestis; duct indistinctly divided by tufts of cilia into sperm- and ova-bearing grooves.

Sperm head sharply pointed, encircled counter-clockwise (from apex) by a spiral blade that completes 5 turns; blade quite weak at base of sperm head, but distorting its apical shaft into a corkscrew-like appearance.

CENTRAL NERVOUS SYSTEM. Nerve ring positioned immediately behind buccal mass, composed of 2 cerebral, 2 pleural, 1 visceral (displaced to right), and 2 pedal ganglia; pleural ganglia separated by short commissures from both cerebral and pedal ganglia.

MANTLE CAVITY. Mantle cavity opens to exterior via a pore at posterior extremity of animal which in life appears as a dorsal slit. Into this small, obesely tubular sac open the intestine (ventral far left); the aperture of the auxiliary respiratory structure, or lung (central left); and the ureteric pore, via a papilla (dorsal far left). Sparsely distributed mucocytes discharge into mantle cavity, the surface of which is not ciliated.

HEART, KIDNEY, AND LUNG. Kidney a thin-walled, irregularly U-shaped sac lying dorsally, just under body wall, in a position corresponding with downward slope at posterior end of (preserved) animal. Of its 2 anteriorly directed limbs, the right one is the longer. Inside wall of right limb is a band of thickened, opaque tissue perforated by reno-pericardial canal, which links kidney lumen with pericardial cavity.

Pericardium discontinuously attached to anterior edge of left kidney limb near midline of slug. Auricle (posterior) frilly on its free edge; ventricle (anterior) smaller, more muscular. Dorsal aorta extends cephalad along midline, losing its identity about level with middle of digestive gland. About level with centre of ventricle a reno-pericardial canal runs posterolaterally into right anterior lobe of kidney.

Lung constructed of numerous bubble-like chambers, or lacunae, separated by flexuous squamose cells (it is not unlike clear, flexible plastic in texture when manipulated with a probe). Lung fuses near its base with wall of kidney, by which it is overlain; elsewhere it is exposed to the haemocoelic spaces. Lung lies anterior to mantle cavity, and presses anteriorly against posterior edge of ovotestis. Aperture to mantle cavity apparently kept open by reinforcing ridges that branch just inside lung, and which are probably the rigid cell walls of the lung tissue here. Outside wall of lung a layer of squamous epithelium, 1-3 cells thick, with sparsely distributed goblet cells. Lacunae filled to a varying degree with an amorphous, non-granular substance containing air bubbles and staining pale purple on dorsal wall of lung and pink on ventral wall. Pink-staining blood lacunae are distributed densely towards posterior extremity of slug, particularly along canal to mantle opening. Further caudad, these lacunae are buried in connective tissue, and do not contribute to the free-hanging organ referred to above as lung, although continuous with it. Other blood lacunae are distributed sparsely through body wall near dorsal surface. Laminae separating dorsal and ventral haemocoelic spaces branch and thread as capillaries betwen lacunae of lung in at least one place.

Type data. **Holotype** (M67825) and 60 **paratypes** (M67826) in National Museum, Wellington, New Zealand. Five paratypes in Australian Museum, Sydney; Field Museum of Natural History, Chicago; Zoologisches Institut, Vienna; and British Museum (Natural History), London. Microslides of serial sections in National Museum, Wellington. **Type locality**: between MHWN and EHWS on limestone gravel beach 40 m north of Rhino Horns Point, Kaikoura Peninsula, South Island, New Zealand (42°26'S, 173°42'E); interstitial. Type series selected from material collected 5 December 1979 by B.A. Marshall; other topotypic material examined collected 28–29 August 1971 by I. Mannering and December 1976 by J. van Berkel.

Other records. First Bay, Kaikoura Peninsula, 15 Feb 1972, I. Mannering. Cove just W of Houghton Bay, Wellington City, 11 Dec 1979, F.M. Climo & C.D. Paulin.

Habitat and biology. *S. manneringi* occurs on rocky beaches with steep profiles, often pounded by heavy surf, where the upper part of the intertidal zone is covered by drifts of clean, wave-sorted gravel with particles 2–4 cm in diameter. The gravels are composed of limestone fragments at Kaikoura and greywacke (Mesozoic siltstone and sandstone) fragments at Wellington. These unstable habitats, shifted and sorted by spring tides (particularly during storms), overlie finer sedimentary material or bedrock, depending on local topography. Even on hot summer days the gravel is cool and wet within 20 cm of the surface. Small fragments of algae (mainly red and brown) occur in the gravel interstices; larger fragments (or whole plants) and other jetsam lie on the surface.

The biology of high-shore interstitial habitats on unstable gravel beaches is poorly understood in New Zealand, and *S. manneringi* is the only macro-organism to my knowledge that appears to be restricted to such habitats. Its distribution in New Zealand, and aspects of its biology such as its breeding cycle, have yet to be studied. Some features of its locomotion have been observed, however.

The slug crawls with a gliding motion, and regular contractions of the specialised part of the foot over the pedal mucus gland cause it to exude voluminous amounts of watery mucus (this is clearly visible on a glass slide). A bubble of air is usually trapped in the posterior chamber of the mucus gland when the animal is crawling.

If one tries to dislodge a slug from a glass slide with a probe (viewing from above, through the slide to the sole of the foot), the area around the head, over the mucus gland, and about the width of the mucus gland velum further back presses against the slide. The intervening area of the foot—posteriorly adjacent to the deep, recessed chamber of the mucus gland—contracts dorsally, presumably forming a partial vacuum. The structures involved in this anterior 'sucker' closely resemble in shape those on the ventral surface of the intertidal clingfish (family Gobiesocidae). This anterior adhering mechanism fastens the slug to a smooth surface more strongly than do the local contractions of the posterior part of the foot.

DISCUSSION

Table 1 outlines the morphological characteristics of the families that I interpret as composing subclass Gymnomorpha. The absence of any clear correlation in sets of characters anywhere in the table strongly suggests a polyphyletic origin for the gymnomorph level of organisation.

The characteristics of *Smeagol manneringi* that I use to interpret it as a gymnomorph, and not a pulmonate, are:

(i) general body form;
(ii) structure of the nidimental complex of the reproductive system;
(iii) apparent homology of the smeagolid and onchidiid auxiliary respiratory structures, in light of the acceptance of onchidiids as gymnomorphs by proponents of that subclass concept.

The characteristics of *S. manneringi* that I use to interpret it as a representative of a new order are:

(i) the only gymnomorph with a diaul-syntremous reproductive system;
(ii) the only gymnomorph with a visceral ganglion on the right;
(iii) the distal concentration of prostatic tissue;
(iv) the suite of characteristics adapting *Smeagol* to an interstitial life style, including loss of eyes and tentacles and development of an adhesive sucker.

S. manneringi might be looked upon as an extremely modified onchidiid, yet morphological displacement from the ancestral condition (presumably, in this instance, a surface-dweller) reaches a level at which it is more useful to establish a separate category. The characters defining Smeagolida are, in my opinion, as strong as those defining the other orders in subclass Gymnomorpha. Any similarity that *Smeagol* may be thought to show to an onchidiid revolves around the proposition that they are both gymnomorph slugs. With minor variations, all gymnomorphs have the same type of alimentary canal and radula, the same external shape, and the same type of body wall—all impositions arising from the probability that their marine ancestors were already highly detorted slugs that had to adapt to a terrestrial life-style.

I consider the nidimental complex of *S. manneringi* to be unlike that of any pulmonate, but Rudman (1970) feels that the diaulic reproductive system (androdriaulic of Ghiselin (1966)) is suggestive of the pulmonate level of organisation. Details of the reproductive system of *S. manneringi* show, however, that this diaulism is not at all like the stylommatophoran pulmonate condition, in which the prostate is proximal (as it is, coincidentally, in Onchidiidae); the nidimental complex of *Smeagol* is composed only of albumen and mucus glands, and the prostate is distal, concentrated next to the penis. I doubt that androdiaulism is any more a feature of the 'pulmonate' condition than it is of the 'opisthobranch' condition; but further discussion is futile until various points—beyond the purpose of this paper—are clarified.

The clues needed to unravel the phylogenetic relationships of the Gymnomorpha reside in an elucidation of the homology (or not) of the pulmonate and gymnomorph lungs and the relationship of cephalaspid opisthobranch pallial glands to the gymnomorph lung.

ACKNOWLEDGMENTS

For useful comments at various stages in the preparation of this paper I thank Prof. W. C. Clark (Dept of Zoology, University of Canterbury), Drs M. C. Miller and R. C. Willan (Dept of Zoology, University of Auckland), Dr W. B. Rudman (Australian Museum, Sydney), Dr L. Salvini-Plawen (Zoologisches Institut, Universitat Wien), and my colleagues Dr J. C. Yaldwyn and Mr B. A. Marshall. Mr A. Hoverd (Histology Laboratory, Victoria University of Wellington) assisted greatly in the preparation of microslides.

REFERENCES

BAKER, H. B. 1955: Heterurethrous and aulacopod. *The Nautilus 68(4)*: 109–12.

BOETTGER, C. R. 1955: Die systematik der euthyneuren schnecken. *Zoologischer Anzeiger 18* (Suppl. Vol.), Leipzig, 1955: 233–80.

FORCART, L. 1953: The Veronicellidae of Africa (Mollusca, Pulmonata). *Annales du Musée Royal du Congo Belge, Tervuren (Ser. 8), Sciences Zoologiques 23*: 6–110.

FRETTER, V. 1943: Studies in the functional morphology and embryology of *Onchidella celtica* (Forbes & Hanley) and their bearing on its relationships. *Journal of the Marine Biological Association of the United Kingdom 25(4)*: 685–720.

GHISELIN, M. T. 1966: Reproductive function and the phylogeny of opisthobranch gastropoda. *Malacologia 3(3)*: 327–78.

MINICHEV, JU. S. 1975: A taxonomic position of the Soleolifera (Gastropoda). *Biologiya Morya (Vladivostok) 1*: 31–8 [Russian – English summary].

MINICHEV, JU. S.; SLAVOSHEVSKAYA, C. V. 1971: Peculiarities of evolution of the renopericardial complex in terrestrial Pulmonata. *Zoologicheskiy Zhurnal (Moscow) 50*: 350–60 [Russian – English summary].

MINICHEV, JU. S.; STAROBOGATOV, YA. I. 1975: On the systematization of euthyneuran snails. Pp. 8–11 in I. M. LIKHAREV (Ed.), *Molluscs: Their System Evolution and Significance*. Abstracts from Fifth Meeting in the Investigation of Mollusca, Zoological Institute, Academy of Sciences, U.S.S.R. [Russian – English list of contents].

OBERZELLER, E. 1970: Ergebnisse der österreichischen Neukaledonien-Expedition 1965. Terrestrische Gastropoda, 2: Veronicellidae und Athoracophoridae. *Annalen des Naturhistorischen Museums in Wien 74*: 325–41.

PETERELLIS, L. S.; DUNDEE, D. S. 1969: *Veronicella ameghini* (Gastropoda): reproductive, digestive and nervous system. *Transactions of the American Microscopical Society 88*: 547–58.

PILSBRY, H. A. 1948: "The Land Mollusca of North America (North of Mexico)", Vol. 2. *Academy of Natural Sciences of Philadelphia Monograph* 39.

RUDMAN, W. B. 1970: "Studies on the bullomorph opisthobranchs". Unpubl. Ph.D. thesis, University of Auckland, New Zealand.

SALVINI-PLAWEN, L. V. 1970: Zur systematischen Stellung von Soleolifera und *Rhodope* (Gastropoda, Euthyneura). *Zoologische Jahrbücher; Systematik, Okologie und Geographie der Tiere 97*: 285–99.

——— 1979: A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia 19(2)*: 249–78.

SOLEM, A. 1959: Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana, Zoology 43(1)*.

——— 1978: Classification of the land Mollusca. Ch. 2 in V. FRETTER & J. PEAKE (Eds). *Pulmonates*; Vol. 2A, *Systematics, evolution and ecology*. Academic Press, London.

——— 1979: A theory of land snail biogeographic patterns through time. Ch. 10 in S. VAN DER SPOEL, A. C. VAN BRUGGEN, & J. LEVER (Eds). *Pathways in Malacology*. Junk, The Hague.

VAN MOL, J. J. 1967: Étude morphologique et phylogénétique du ganglion cérébroïde des Gastéropodes Pulmonés (Mollusques). *Mémoires de l'Académie Royale de Belgique, Classe des Sciences 37(2)*.