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Anatomical Studies of Three Species of *Ouagapia*
(Pulmonata, Agnatha, Paryphantidae)

By **YOSHIO KONDO**

BERNICE P. BISHOP MUSEUM

INTRODUCTION

This paper presents the results of anatomical studies of three species of land snails of the Paryphantidae collected on Viti Levu in Fiji, Tau and Tutuila in Samoa, and Kusaie in the east Carolines. They are *Ouagapia ratusukuni*, *O. gradata*, and *O. oualanensis*. These three species are tentatively located in the genus *Ouagapia* Crosse, for until the type of the genus, *O. raynali*, and related species, together with the species of *Ptychorhytida* Moellendorff (type, *P. beraudi*), are anatomically studied, the true position of the three species under consideration remains uncertain. Furthermore, there may be room for subgeneric divisions among the three, the chief difference being oviparity (Fijian and Samoan spp.) and ovoviviparity (Kusaie sp.). In *Ptychorhytida inequalis* a uterus may contain as many as a dozen eggs, whereas in *O. ratusukuni* the uterus never contains more than a single egg. Two were found in the only pregnant specimen of *O. gradata*. In *O. rapida* (7162) and *O. oualanensis* the female pouch contains only single embryos. The anatomy includes (a) the external parts, (b) pallial complex, (c) genitalia, (d) the central nervous system, and (e) the digestive system up to the oesophagus. A number of species of this genus are reported from New Caledonia, the New Hebrides, and the Solomons; but a review of available literature reveals that no comprehensive anatomical studies have been made of any of them. Consequently, the true relationship among the Melanesian, Micronesian, and Polynesian species remains obscure.

All of the specimens discussed are in the collection of Bishop Museum.

I am indebted to Dr. C. Montague Cooke, Jr., who guided this research. I was able to draw freely upon his knowledge of the shells and their literature.

REVIEW OF LITERATURE

Ouagapia Crosse belongs to the carnivorous family of land snails, Paryphantidae (= Rhytididae), which includes the genera *Paryphanta*, *Rhytida*, *Wainuia*, *Delos*, and *Schizoglossa* (New Zealand, Australia); *Macrocycloides* (New Zealand, Australia, Solomons, Moluccas, South Africa); *Diplomphalus* (New Caledonia); *Priodiscus* (Seychelles); *Nata* and *Natalina* (South Africa).

Semper (26)¹ makes a casual anatomical reference to *Patula* (= *Ouagapia*) *gradata* Gould. Because of the absence of a jaw and because of the type of teeth, he correctly transferred it from the Endodontidae to the Rhytididae. However, he neither described nor figured these organs. Fischer (9, pp. 6-9, figs. 1-6 on pl. 3) described and figured the genitalia, central nervous system, and teeth of *Helix* (= *Ptychorhytida*) *inequalis* Pfeiffer together with the animal and teeth of *H.* (= *Ptychorhytida*) *multisulcata* Gassies (9, p. 9, fig. 7) and *H.* (= *Diplomphalus*) *cabriti* Gassies (9, pp. 9-10, figs. 8, 9). In *H. inequalis* the verge (penis) is described as a little elongate, sub-cylindrical, attenuate, muscle terminal. Vagina (free oviduct) quite long, thick, cylindrical. Matrice (uterus) very thin, distended with eggs to about a dozen, the largest being nearest the vagina. Egg with solid calcareous shell, greatest diameter 3 mm. Embryos with two whorls were found in the eggs. Glande albuminipare (albumin gland) very small and like a cluster of grapes. Poche copulatrice (spermatheca) rounded, small, with medium-long stalk. No accessory organs. The hermaphrodite gland is not mentioned and no prostate is described or figured. Figure 6 shows a central nervous system with extremely long cerebro-pleural and cerebro-pedal connectives, the paired ganglia strongly adnate. Enervation undescribed. Digestive system of carnivorous type, pharynx with two retractors. Teeth aculeate, unicuspid, arcuately disposed, without centrals, two first teeth small, the following of medium size, marginals very small, formula 12-0-12 × 40 for *H. inequalis*, 23-0-23 × 63 for *H. multisulcata*, 16-0-16 × ? for *H. cabriti*.

¹ Numbers in parentheses refer to Bibliography, p. 248.

The literature on related genera is extensive. Suter (28, pp. 770-789) condenses the anatomical notes on all the New Zealand genera. Hedley (12) describes and figures the animal, genitalia, digestive system, and teeth of *Schizoglossa*. Godwin-Austen (10) figures the interior of the penis of *Paryphanta hochstetteri*. Woodward (31) also figures a penial section and gives a good description of the buccal muscles of *Natalina caffra*. Murdoch (16) treats the anatomy of *Rhytida*, *Rhenca*, *Schizoglossa*, *Paryphanta*, and *Natalina*, and three species of *Paryphanta* (17, 18, 19). Powell (25, p. 24, fig. 2) summarizes the dentition of Paryphantidae. Of the African genera, early researches were done by Pilsbry (21, 22, 23). Watson (30) describes and figures the body lobes, kidneys, genitalia, and teeth of *Nata* and *Natalina*.

MATERIAL AND METHOD

The animals of *Ouagapia* were preserved by Cooke's method. They were drowned in fresh water 12 to 18 hours, alcoholized for a half hour to one hour in 40 to 50 percent alcohol, then pickled in 40 to 50 percent alcohol in the field, extracted, and then finally preserved in the laboratory in 75 percent alcohol. Except for slight shrinkage caused by the alcohol, the animals were well preserved.

Snails were dissected in a small water-filled pan (depth of water 5 mm.) under a binocular microscope illuminated by condensed sunlight. In each species at least 3 specimens were dissected to note genitalial variations alone. Additional specimens were dissected for their digestive and nervous systems. In each species at least 5 specimens were examined.

Illustrations and their measurements were made with the camera lucida, due consideration being given to the height of the pan from the stage. The scales are the averages of several projected measurements. All drawings are natural except that of the central nervous system of *O. ratusukuni* which is semi-diagrammatic, insofar as the connectives are concerned.

In extracting the teeth, the pharynx was first boiled in 15 percent potassium hydroxide for 15 to 30 minutes. I followed a modified Peile's technique in staining and mounting the radulae. The radulae were (a) oxidized in a boiling solution of water, potassium permanganate, and 75 percent acetic acid, (b) bleached by adding potassium oxalate, (c) stained with methyl violet, dissolved in 50 percent alcohol, from one half to one hour, and (d) mounted in canada balsam or gum

damar. The teeth were figured and measured with a camera lucida. A minimum of four slides was made for each species.

Because I was unable to locate any complete study of the nervous system of this family, I used as a guide Baker's dissection and description (2) of *Microcystis* (*Microcystis*) *ornatella* (Beck).

The following abbreviations, used on the figures, are contractions of the conventional terms and are as self-explanatory as possible.

ABD: abdominal	OÆ: oesophagus
A G: albumin gland	OV: ovum
ANT: anterior	P: penis
AT: atrium	PAR: parietal
AU: auricle	PED: pedal
Bucc: buccal	PH: pharynx, pharyngeal
C: central	PIL: pilaster
CA: carrefour	PLEU: pleural
CER: cerebral	POST: posterior
CONN: connective	PR: prostate
DORS: dorsal	PROB: proboscis
EPI: epiphallus	P R: penial retractor
GANG: ganglion	P SH: penial sheath
GL: gland	REF: reflexed
G O: genital orifice	RET: retractor
H G: hermaphrodite gland	RT: right
H D: hermaphrodite duct	SAL: salivary
INF: inferior	SH: shell
INT: intestinal	SP: spermatheca
KD: kidney	STIM: stimulator
LAB: labial	SUP: superior
LAP: lappet	TA: talon
LAT: lateral	TENT: tentacle, tentacular
Lt: left	URE: ureter, ureteric
M: mouth	UT: uterus
MEMB: membrane	VAG: vagina
MUSC: muscle, muscular	VD: vas deferens
NUC: nuchal	VENT: ventral
O: orifice	VL: ventricle

Genus **OUAGAPIA** Crosse, 1894

Agnaeous, carnivorous snail with protrusible proboscis, without epipodial groove and caudal foss; genital opening at right side on midline below mantle collar; with two left mantle lappets and one right lappet. Pharynx strongly muscular, cylindrical, as long as body cavity, with one strong retractor. Radula spatulate, the anterior half the broader, inwardly bent at the middle; teeth acute, unicuspid, with narrow oblong basal plate. Genitalia simple, hermaphrodite gland composed of few saccate lobes (2 or 3 in Polynesian spp.), hermaphrodite duct convoluted, spermatheca short, vagina short, penis small to large with or without epiphallus, retractor terminal, right tentacle free of penio-oviducal angle.

"Shell widely and perspective umbilicate, discoidal, thin, spirally obscurely striate above, somewhat shining, nearly smooth below, glossy, olive-greenish, irregularly speckled with brown maculations; spire nearly flat; suture strongly impressed, channelled; aperture subhorizontal, ovate-lunate; peristome simple, delicate, acute. Animal unknown." (Crosse, Jour. de Conch. p. 203, 1894.)

Key to species of *Ouagapia*

1. Penis clavate, with epiphallus and large fistlike verge; adult and juvenile radulae with centrals, formula 20-1-20 to 23-1-23 \times 86-88 rows.....**O. oualanensis.**
 2. Penis attenuate, epiphallus absent.....3.
 3. Penis bottle shaped, diameter of base about $\frac{1}{3}$ its length, with large stimulator pilaster; adult and juvenile lacking centrals, formula 13-0-13 or 14-0-14 \times 67-80 rows.....**O. gradata.**
- Penis nearly linear, attenuate only slightly at tip, diameter of base about $\frac{1}{6}$ its length, without verge or stimulator-pilaster; adult radula without central, formula 12-0-12 or 13-0-13 \times 55-66; juvenile with central, formula 12-1-12 or 13-1-13 \times 55-66 rows.....**O. ratusukuni.**

1. *Ouagapia ratusukuni* Cooke, B. P. Bishop Mus., Occ. Papers 17(9): 91-92, 1942 (figs. 1, *a-g*; 2, *a-d*; 5, *a*).

Shell "discoidal, umbilicus shallow and very wide, epidermis very thin, glossy, somewhat deciduous, olive buff in color, marked with widely separated narrow, indistinct, brownish bands. Surface (except on smooth embryonic whorls) is marked with very fine, sharp, close striae and is spirally sculptured with rather widely spaced, very fine incised lines. Spire flat. Whorls 4.66, the embryonic increasing rapidly, the rest slowly and regularly, convex, separated by a rather deep suture. The last whorl not descending, well-rounded at periphery. Aperture scarcely oblique, truncate-oval. Peristome very thin, sharp. Height 4, diam. 11.0; apert. vertical 3.8, horizontal 3.1." (Cooke)

Animal (fig. 1, *d*) grayish, strongly and entirely verrucose or warty in contracted specimens but only posterior half so sculptured in those fully expanded, the grooves between the verrucosities deep. Epipodial grooves and caudal foss absent. Both superior and inferior tentacles present. Genital orifice (G O) (fig. 1, *d*) on right midline below mantle collar. Proboscis (PROB) (fig. 1, *d*) or introvert protruded and bent ventrad in fully expanded specimens, integument thin, mouth small. Pedal gland opening (PED GL O) (not labeled in fig.; see fig. 3, *c*) between foot and snout at level of inferior tentacles; gland oblong, 0.75 length of body, opening anteriorly by large transverse orifice and posteriorly by tube descending and emptying into podial tissues, the tube with a large bulge at its junction with gland and a smaller bulge farther below. Foot sole unpigmented, flat, transversely wrinkled, its edges strongly wrinkled posteriorly; tail sharp, pointed.

Mantle (fig. 1, *g*) 4 \times length of kidney, narrow, unpigmented; collar with two left lappets and one right (LT DORS LAP, LT VENT LAP, RT LAP). Lappets inconspicuous, small, thin, placed near anterior margin of collar, the left dorsal and right lappets placed near pulmonary orifice. On the posterior margin of collar is an arcuate group of large transparent cells (GL) (see fig. 1, *g*, fig. 1, *b*) oval, round, or irregularly elongate, which may tentatively be named the ostracum or Eckardt's gland (27, p. 823). [Pilsbry (24, p. 310, fig. 2) figures such a

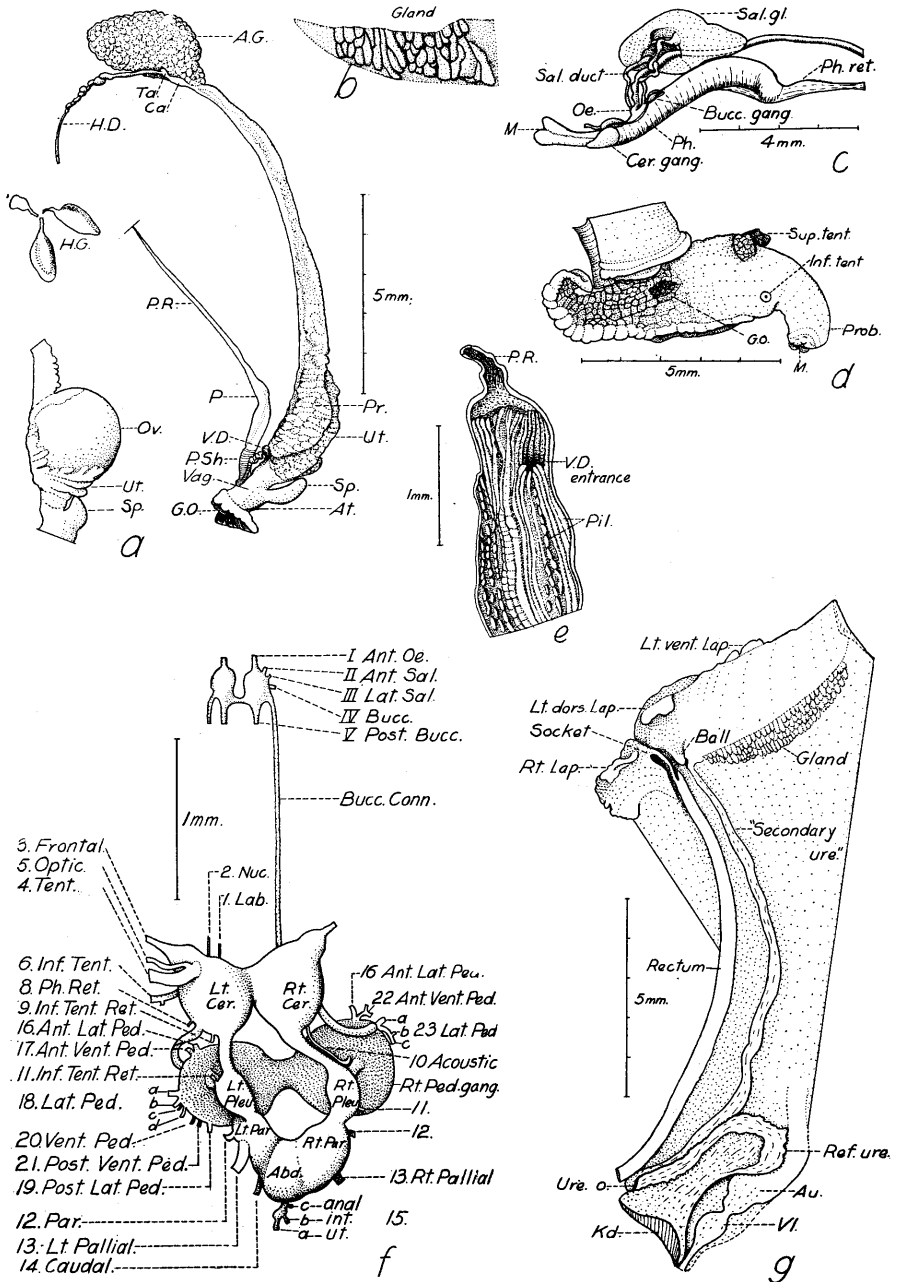


FIGURE 1.—*Ouagapia ratusukuni*: a, genitalia, one gravid; b, closeup of mantle gland, in part; c, digestive system; d, animal, in part; e, interior of penis; f, central nervous system, semi-diagrammatic; g, pallial complex.

gland in *Cochlicopa lubrica* without naming it. Baker (1, pl. 14:9) illustrates similar glands in *Pristiloma (Pristinoides) lansingi* and (pl. 13:1) *P. (Ogari-discus) subrupicola subrupicola*, also without naming it. Simroth and Hoffmann (27, pp. 97, 178, 821) describe several mantle glands, the one approximately that of *O. ratusukuni* appearing to be Eckardt's gland for secreting material for the periostracum.]

Kidney (KD) (fig. 1, *g*) triangular; ureter emerging at level of auricle and running anterior to apex thence reflexing posteriorly on the left side (REF URE), exhausting into shallow furrow or pseudo "secondary ureter" at base of kidney via uretral orifice (URE O).

The pseudo "secondary ureter" is a shallow furrow covered by a thin membrane composed of squamous cells and connective tissues. It leads anteriorly to the pulmonary orifice, emptying below a fleshy protuberance (ball, in fig. 1, *g*). The tube is so called because it is not merely a simple furrow but consists internally of some scattered, short, low, whitish folds. Internally, the kidney consists of heavy, spongy, yellowish, longitudinal folds; the reflexed ureter of a few short, pointed, whitish, longitudinal folds.

Pulmonary orifice appears to be somewhat specialized. Deducing from structural peculiarities, the surface seems to be constructed to serve the urinary, defecatory, and breathing purposes individually or simultaneously. The anal aperture exits via a rather deep channel. To its right is a fleshy protuberance (ball, fig. 1, *g*) which, in conjunction with the angle of the bridge (the tissue composing ventral floor of pulmonary orifice), forms a shallow trench which appears to serve as a urinary channel. To the left of the anus is a deep pocket (socket, fig. 1, *g*) into which the ball fits snugly. Posteriorly of the socket a channel leads back into the lung chamber, apparently the air channel. The ball and socket device is evidently a locking mechanism used for isolating the pulmonary cavity from any unfavorable external conditions.

Digestive system (fig. 1, *c*) specialized for carnivorous habit. Mouth (M) small, simple; pharynx (PH) strongly muscular, cylindrical, narrow, as long as body cavity; pharyngeal retractor (PH RET) strong, off columellar muscle, attached posteriorly-ventrad but continuing anteriorly to nearly midpoint. Cerebral ganglia (CER GANG) anteriorly of oesophagus in expanded animal; oesophagus (OE), salivary ducts (SAL DUCT), and buccal ganglia (BUCC GANG) on dorsal anterior fourth of pharynx. Salivary gland (SAL GL) large, ovate, with long left and short right lobes; oesophagus small, passing between salivary gland lobes; intestine curving several times, emptying into large stomach just posteriorly of albumin gland; liver extensive, occupying entire apical half of animal, whitish, spotted with pearly globules. Radula spatulate, anterior half the broader, bent outwardly in the middle, with a long radular cartilage underlying it.

Teeth formula in adult 12-0-12 \times 55-66 to 13-0-13 \times 55-66; in juvenile 12-1-12 \times 55-66 to 13-1-13 \times 55-66 rows V-shaped, angle about 35 degrees. All teeth (fig. 2) pointed posteriorly, aculeate, unicuspid, sharply pointed, curved apically; basal plates narrow, roughly oblong. Centrals (C) (fig. 2, *a, b, c*) when present, 0.25 length of first tooth, the cusp low, not projecting beyond posterior point of plate, the point not sharply pointed; in metaneanic specimens (whorls 3 to 3.75) variable in shape, cusps pointed or blunt and curved to left (fig. 2, *c*). A para-metaneanic abnormal radula was dissected (fig. 2, *a*), formula 13-1-12. Number 2 on the right is apparently a fusion of 2 and 3, only the bases of which are separate. Number 12, left, has a rounded point which is often

medially cleft. This is probably an age factor. Admedians 10, subequal; marginals 2, diminishing.

Nervous system (fig. 1, f). Numbers correspond to designation on figure. Except where indicated, the nerves were followed from the left ganglion of the pair.

Buccal ganglion, right

Situated on dorsal surface at oesophageal exit; commissure from medio-latero-ventral floor of cerebral ganglion.

Gives off:

- I. Anterior oesophageal, enervating oesophagus just after its exit from dorsum of pharynx.

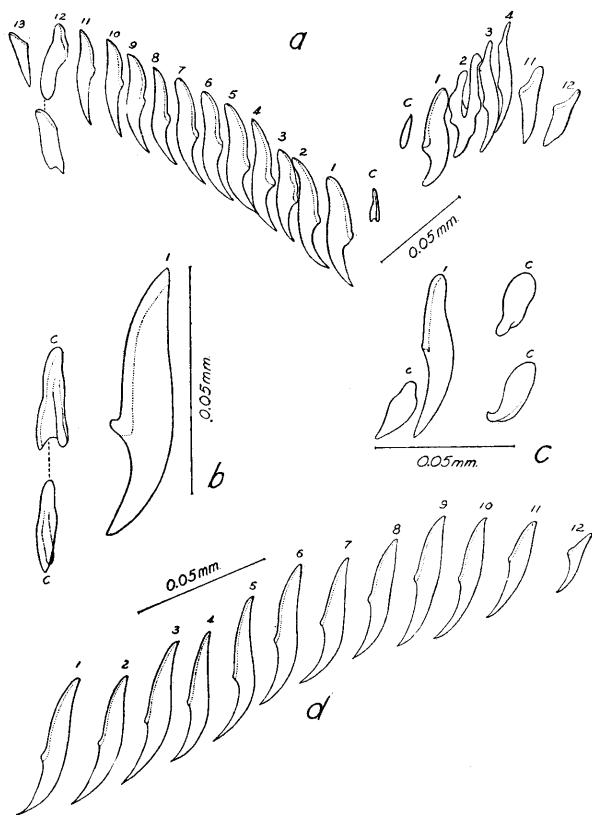


FIGURE 2.—*Ouagapia ratusukuni*: a, abnormal juvenile teeth, with central, parametaneanic; b, closeup of central (lateral and dorsal views) and number 1 tooth, parametaneanic; c, three centrals and number 1 tooth of metaneanic; d, normal adult teeth.

- II. Anterior salivary, attaching to salivary duct just before latter enters dorsum of pharynx.
- III. Small lateral salivary, attaching to duct at posterior plane of buccal ganglion.
- IV. Large buccal nerve, from ventrum of ganglion, attaching immediately to dorsum of pharynx.
- V. Posterior buccal (odontophoral ?), inserting soon into dorsum of pharynx.

Cerebral ganglion

Gives off:

1. Labial, from mid-ventrum directly anterior to mouth. 3 branches: one to pharyngeal protractor, two to labial parts.
2. Nuchal, from laterad of labial origin, directly anterior. 2 branches: one to pharyngeal protractor, the other to nuchal membrane.
3. Frontal to base of ommatophore, branching, one to ommatophore, the other to integument at base of ommatophore.
4. Tentacular, from dorsum of cerebral ganglion to superior tentacle.
5. Optic, branching just above base of tentacular and anastomosing with a nerve branch off inferior tentacle.
6. Inferior tentacular, large, soon giving off two small branches, one to inferior tentacular protractor, the other anastomosing with optic (see 5).
7. Not shown in figure. Inferior tentacular protractor, a small nerve from ventrum of ganglion next to origin of labial.
8. Small pharyngeal retractor off base of cerebro-pedal connective, to bundle of muscle at posterior end of buccal mass.
9. Inferior tentacular retractor, a small nerve between cerebro-pedal and cerebro-pleural connectives.
10. Acoustic nerve (right).

Pleural ganglion

Gives off:

11. Inferior tentacular retractor, in the left pleural originating above and in the right farther below, and anastomosing with inferior tentacular retractor of cerebral (see 9).

Parietal ganglion

Gives off:

12. Parietal, to common tentacular retractors and to pedal gland retractors.
13. Pallial. Right pallial goes below penis, over uterus, into integument.
14. Caudal, through columellar muscle, to tail. In one specimen, in place of the caudal, was a salivary-oviducal nerve, to salivary gland, with a branch to mid-oviduct, originating at the very edge of left parietal ganglion.

Abdominal ganglion

Gives off:

15. A tripartite nerve, giving off three nerves (a) upper uterine, (b) intestinal running along artery, and (c) anal, passing under uterus to the right side. A large bulge characterizes this nerve. In second specimen not tripartite but with one large anal sinking into integument below penis, giving one branch to upper uterus. Next to it a small intestinal which follows artery posteriad.

Left pedal

Gives off:

16. Anterior lateral pedal, following left dorsal angle of pedal gland to side of head.
 17. Anterior ventral pedal, off same place as 16 but ventrad, to foot.
 18. Large lateral pedal trunk with 4 immediately branching nerves to (a) side of head, (b) slightly posterior of side of foot, (c) below b and further posterior of it to side of foot, and (d) to posterior upper foot.
 19. Posterior lateral to posterior wall of visceral stalk.
 20. Ventral pedal, which sinks directly below to foot.
 21. Posterior ventral, also sinking directly below but turning posterior to 20.
- Right pedal.* Nerves are similar to left pedal except in anterior ventral and lateral trunk.

Gives off:

22. Anterior ventral pedal, differing from 17 in having 2 basally connected nerves which sink to foot, one behind the other.
23. Lateral trunk with (a) and (b) branches to side of foot and (c) to genitalia, a branchlet crossing anterior of genitalial base to integument, another crossing behind, going also to integument, and 3 branchlets to penis, distributing finely to penial sheath, penial base, etc.

Genitalia simple (fig. 1, *a*); right tentacle free, passing to left of penis. Penis enervated by pedal ganglion. Species apparently oviparous, 5 animals with one egg each were counted among 7 adults, none with embryo; egg (fig. 5, *a*) orbiculate, diameter 2.20 mm., height 1.70 mm., one face a little flatter than the other. Hermaphrodite gland (H G) bi- to trilobed (each lobe globular in paraneanic, whorls: 4-4.5), roughly oblanceolate in outline in near-adults with 2 or 3 sides partially collapsed inward, white globules (ova?) visible from exterior: (Unfortunately no fully adult animal was preserved entire and only a few young specimens were entire. Consequently only 2 hermaphrodite glands were extracted. Of these one had a small third lobe and the other had only two lobes). Hermaphrodite duct (H D) small, convoluted and enlarged in the middle. Talon (TA) and carrefour (CA) simple. Albumin gland (A G) ovoid, follicles erect, numerous. Vas deferens (V D) and uterus (U_T) apparently separate immediately but are closely adnate until free oviduct. Prostate (P_R) composed of prostrate, digitate follicles lying transversely over lower and bulging part of uterus. Uterus (U_T) long, narrow above but gradually enlarging below, entirely glandular or sacculate. Free oviduct, vagina (V_{AG}), and atrium (A_T) very short. Spermatheca (S_P) simple, short, clavate; in gravid individual a mere projection. Penis (P) nearly linear, apically pointed, with thin penial sheath (P_{SH}) which covers part of free vas deferens. No epiphallus; retractor (P_R) apical, terminating in nuchal membrane. Vas deferens (V D) off lower margin of prostate, convoluted in free part, adnate to penis from base to near apex. Internally, the penis (fig. 1, *e*) consists of numerous (14 to 16) longitudinal folds or pilasters (P_{IL}) which under stress (such as pinning for mounting) break down into numerous bosses.

Fiji: Viti Levu, Nandarivatu in dirt under rotten logs, damp, alt. 3,000-3,600 ft., 10035², type; dissected 178846, 178847, 178848; (Lapham Expedition, Sept. 2, 1938).

² All specimen numbers refer to Bishop Museum collection.

O. ratusukuni was found at Nandarivatu, northern Viti Levu, within a radius of five miles. This species lives on the ground; and at the time of discovery, it was ingesting the animals of a species of diplommatinoid snail (length 2.5 to 3 mm.). In a decayed log another colony was feeding on the eggs of a large zonitoid snail, probably *Orpibella pfeifferi*. The eggs were punctured and their contents devoured.

2. *Ouagapia gradata* (Gould), 1846 (figs. 3, *a-e*; 5, *c*).

Helix gradata Gould, Boston Soc. Nat. Hist., Proc. 2: 172, 1846, Tongataboo; U. S. Expl. Exped., Mollusca and Shells 12: 49, pl. 3; 48, 48a-48c, 1852, Tonga Islands.

Shell "planorboid, convex above, cup-shaped beneath, thin, shining, with coarse, regular, and crowded striae, crossed by interrupted, equidistant revolving lines. Whorls five, separated by a deeply channelled suture, the outer whorl a little angular at periphery; beneath sharply angular as it borders the broad umbilicus, and so are each and all the whorls as they present their edge in the vortex: aperture circular or a little transverse, slightly modified by the last whorl: lip simple, somewhat everted at the umbilicus. Colour brandy-red, somewhat rayed by unequal and irregular stripes of pale yellow. Diameter half an inch; axis one-fifth of an inch." (Gould, 1852)

Animal (fig. 3, *c*) similar to *O. ratusukuni*, diffusely pigmented; epipodial groove and caudal foss absent. Some specimens (3 in 50) verrucose, most of them nearly smooth; verrucosities at hinder end of foot, proportionately larger and less numerous than in *O. ratusukuni*. With superior and inferior tentacles, both large, the superior not granulose as in the Fijian species. Genital orifice on midline below mantle collar. Proboscis protruded but not usually bent ventrad in fully expanded specimens, somewhat cylindrical, thinly integumented; mouth rather large. Pedal gland orifice (PED GL, O) large, opening at anterior margin of foot below base of snout. Foot sole flat, transversely wrinkled, the edges broadly wrinkled, tail not very sharply pointed.

Mantle (fig. 3, *d*) broad, $3.5 \times$ length of kidney, similar to that of *O. ratusukuni*; collar much narrower and mantle gland (GL) occupying nearly entire left side, cells of gland not transparent but opaque, not clear cut as in *O. ratusukuni* (one specimen with cells turned horny, probably parasitized). Left dorsal and ventral mantle lappets small, closer to each other than those in *O. ratusukuni*; right lappet broader.

Kidney (KD) (fig. 3, *d*) broadly triangular, ureter emerging on right side and nearer to apex than in Fiji species but still at level of auricle. Ureter reflexed (REF URE) posteriad, opening into shallow indistinct uncovered groove which terminates near anus. Pulmonary orifice simple, with ball and socket device but not clearly demarcated as in *O. ratusukuni*.

Digestive system similar to Fijian species. Pharynx cylindrical, as long as body cavity; single retractor smaller and weaker. Radula spatulate, anterior half broader, medially and outwardly bent.

Teeth (fig. 3, *a*) formula 13-0-13 or 14-0-14 \times 67-80, mostly the latter; rows V-shaped, angle about 45 degrees. All teeth pointed posteriad, aculeate, uni-

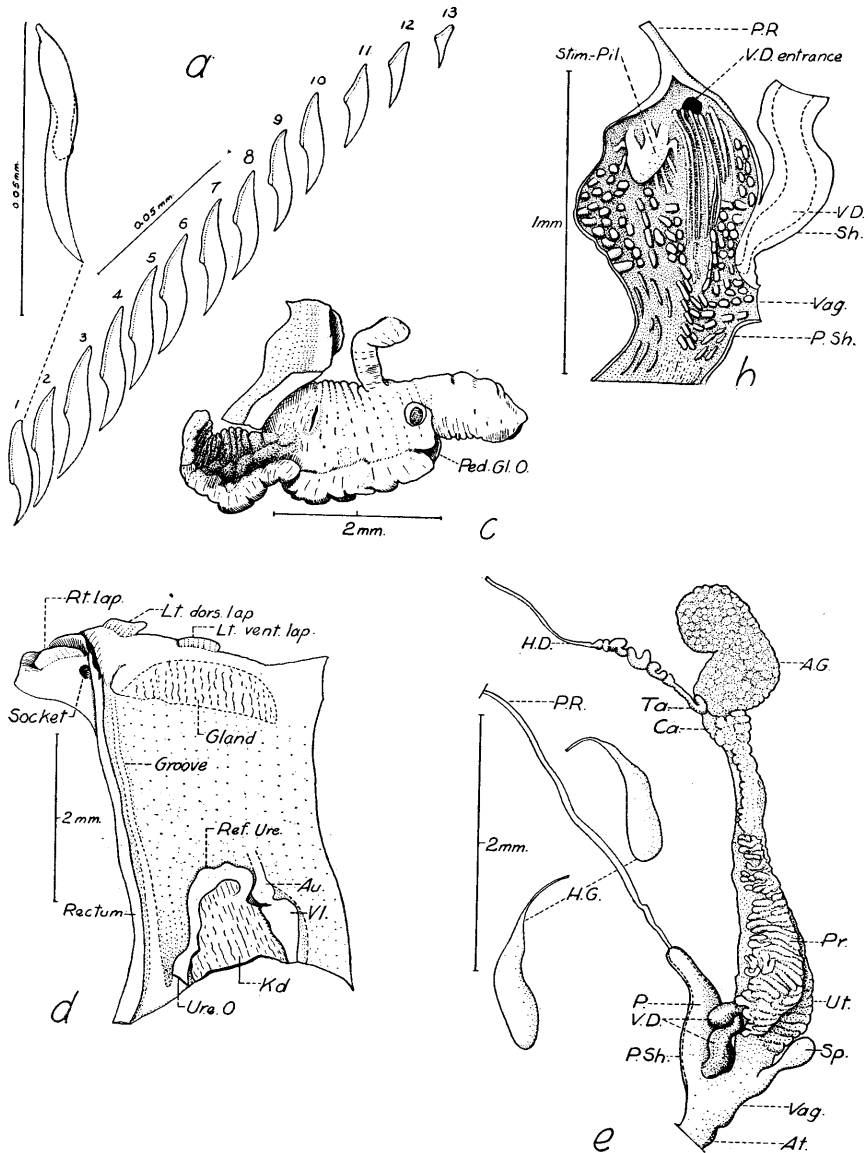


FIGURE 3.—*Onagapia gradata*: a, teeth, right half with closeup of dorsal view of number 1; b, interior of penis; c, animal, in part; d, pallial complex; e, genitalia.

cuspid, but not as sharply pointed or as strongly curved as in *O. ratusukuni*; basal plate narrow, oblong. Admedians 10, nearly equal in size; marginals 3, diminishing in size outwardly. Juveniles (whorls: 3-3.5) without centrals in contrast to *O. ratusukuni*.

Nervous system similar to *O. ratusukuni*, deviating only slightly as follows:

15. Anal passes below genitalia, giving one branch to mid-oviduct.
18. Laterals 2 and 3 united basally; 4 ventral pedals.
23. No lateral trunk; penial nerve given off alone from side of right pedal at foot of pleuro-pedal connective, one branch to genital pore region, the other to penis and atrium.

Genitalia (fig. 3, *e*) simple, right tentacle free, to left of penis; penis enervated by pedal ganglion. Species oviparous. Only one of 90 snails examined pregnant, with two eggs in oviduct. Egg (fig. 5, *c*) orbiculate, diameter 1.20 mm., height 0.90 mm., one face definitely flatter than the other. Hermaphrodite gland (H G) bilobed, the sacs elongate, smooth, tapering from rounded base to efferent duct. Hermaphrodite duct (H D) convoluted and enlarged in the middle. Talon (TA) small, carrefour (CA) rounded. Albumin gland (A G) ovoid, composed of numerous short erect follicles. Prostate (PR) commencing some distance below carrefour gradually increasing in size with uterus (Ur), follicles large, digitate and lying transversely. Vas deferens (V D) and uterus (Ur) strongly adnate until former emerges free at level of spermatheca (SP). Free oviduct, vagina, and atrium (AT) more distinct and proportionately longer than in *O. ratusukuni*. Lower uterus strongly wrinkled or sacculate. Spermatheca (SP) short, clavate, strongly adnate to uterus. Free vas deferens sheathed, bulging, looping once before adhering to base of penis, not fastened to penis with tissues as in *O. ratusukuni*. Penis (P) bottled, sheathed, basal half broad, suddenly tapering to narrow neck and head. Internally (fig. 3, *b*), penis is composed of a few longitudinal pilasters (which, under stress, break down into bosses) and a simple large conical stimulator-pilaster (STIM-PIL) below entrance of vas deferens. Base of stimulator-pilaster tapers off into short longitudinal pilasters. Atrium and vaginal orifice studded with bosses and short folds. Penial retractor (PR) apical, thin, long, off columella muscle. In one specimen off membrane of upper uterus.

Samoa: Tutuila, Fagatoga, under damp dead leaves, alt. 800 ft., 85097 and 85098 dissected (Samoan Exped., March 27, 1926). Tau, Faleulu Valley, on damp ground under grass, ferns, and coconut trees, alt. 550 ft.; 188505 dissected (collected by Segisegi for Wray Harris).

As far as the Bishop Museum collection is concerned, the range of this species is circumscribed by the triangle formed by Samoa at the northern corner, Tonga at the southern, and Niuafoou at the western corner. The material in the museum is from the following localities: Tonga: Tongatabu (near Haamonga), Vavau, Eua (Vaigana); Samoa: Tutuila (Fagatoga), Tau (Faleulu Valley), Upolu, Ofu, Savaii (Satana); and Niuafoou. Of these, Eua, in Tonga and Savaii, Ofu, and Tau in Samoa are heretofore unrecorded.

3. *Ouagapia oualanensis* (Pease), 1866 (figs. 4, *a-e*; 5, *b*).

Helix oualanensis, Pease, Am. Jour. Conch. 2: 289, pl. 21, fig. 1 (3 views) 1866, Polynesia [Oualau (Oualan = Kusaie), Pease, Zool. Soc. London, Proc., 475, 1871].

Shell "small, discoidal, thin, shining, plane above, periphery rounded, spire depressed, forming a plane, slightly concave at apex; whorls 3-4, somewhat roughened by radiating striae of growth, concentrically obsolete striated, the last whorl rounded at base, widely umbilicate. Color light greyish-yellow, ornamented with brownish-red zigzag lines or stripes, obliquely, sometimes radiately disposed. Diam. 5, alt. 2 mill." (Pease, 1866).

Animal (fig. 4, *c*) similar to *O. ratusukuni* and *O. gradata*. Epipodial groove and caudal foss absent; tail pointed, lightly grayed on anterior face of visceral stalk; visceral stalk and posterior half verrucose. Superior and inferior tentacles proportionately smaller than those of *O. gradata*, not granulose. Proboscis extruded in fully expanded specimens, cylindrical, thinly integumented, mouth rather large. Pedal gland orifice small. Foot sole narrow, slightly wrinkled transversely, the edges not strongly wrinkled.

Mantle (fig. 4, *b*) proportionately broader and shorter than in *O. gradata*, $3.5 \times$ length of kidney, without pigmentation. Collar without gland. Mantle lappets larger in proportion to collar than either *O. gradata* or *O. ratusukuni*. Left dorsal lappet adjacent to pulmonary orifice, thick; left ventral thin but broad; right lappet wide.

Kidney (KD) (fig. 4, *b*) more broadly triangular than in *O. gradata*. longitudinal folds conspicuous; ureter (REF URE) off kidney at right side and more apical than in *O. gradata*, reflexed posteriad, opening at left angle into shallow indistinct groove without cover and underlaid by a muscular strip (MUSC STRIP).

Pulmonary orifice similar to that of *O. gradata*.

Digestive system similar to those of *O. gradata* and *O. ratusukuni*. Pharyngeal retractor single, large, off columellar. Salivary gland smaller than in other two species, half-moon shaped, the left lobe the longer. Disposition of oesophagus, salivary ducts, and buccal ganglia also similar. Radula spatulate, anterior half the broader, medially and outwardly bent.

Teeth (fig. 4, *a*) formula (20-23)-1-(20-23) \times (86-88). Young with centrals although one specimen was without it. All teeth pointed posteriad, aculeate, unicuspid, curved but not as strongly as in *O. ratusukuni*; basal plate narrow, oblong. Centrals 0.75 the length of first admedian and strongly curved, sharply pointed, unlike that of young *O. ratusukuni*. Admedians about 18, nearly equal in size up to number 10, then smaller to number 18. Marginals of 3 rapidly diminishing sizes, outermost the smallest.

Nervous system not radically different from that of *O. ratusukuni*. Buccal ganglia with similar nerves except in having 2 posterior buccal nerves, the lateral one possibly being the buccal (IV in fig. 1, *f*).

Cerebral

1. Labial from mid-ventrum to mouth parts.
2. Nuchal to integument on anterior basal region of superior tentacle.
3. Frontal to base of ommatophore with optic branch.
4. Large tentacular to superior tentacle.
5. Optic off base of tentacular, adnate to nuchal, recurving at terminus to optic stalk.

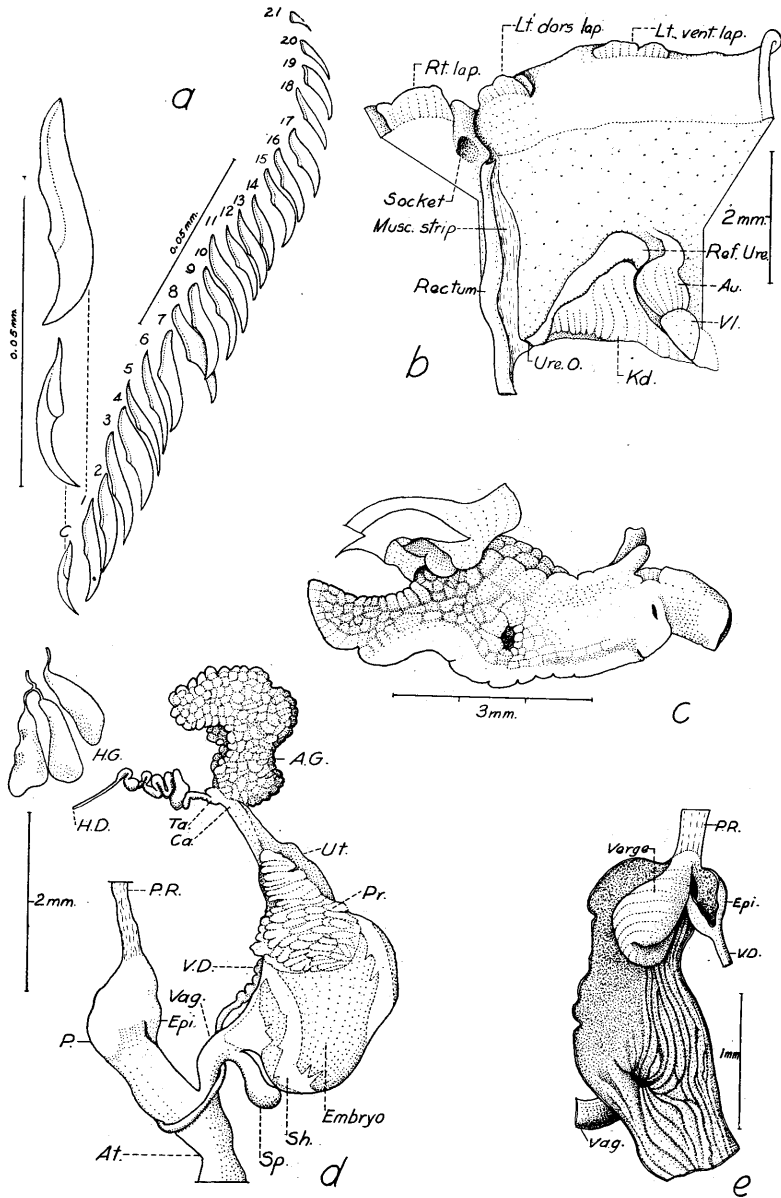


FIGURE 4.—*Ouagapia oualanensis*: a, teeth, right half, with closeups of central and number 1; b, pallial complex; c, animal, in part; d, genitalia; e, interior of penis.

6. Inferior tentacular a little larger than superior.
7. Inferior tentacular protractor (?), from base of 6.
8. Pharyngeal retractor.
9. Inferior tentacular retractor, just above inferior tentacular.
10. Acoustic, between cerebro-pedal and cerebro-pleural to anterior base of latter.

Pleural

11. Inferior tentacular retractor. The left retractor nerve is peculiarly ramified with other nerves. Immediately upon emergence it bifurcates into (a) the anterior which, after sending nervelet to lateral pedal, bifurcates once more and enervates posterior lateral pedal integument and (b) the posterior which, after linking with left pallial, of left parietal ganglion, enervates left inferior tentacular retractor.

Parietal

12. Pallial, crossing over superior tentacle. Right pallial crosses over penis, under uterus, to integument.
13. Caudal, passing through bifurcation point of tentacular retractors, to slit in columellar muscle, to tail.

Abdominal

14. Thin oviducal from apex of ganglion to midoviduct.
15. Anal from directly below 14, under genitalia, to right side of body.
16. Very thin intestinal, following artery posteriad.

Left pedal, with usual dorsal and ventral pedals.

Right pedal, with usual pedals.

23. Lateral pedal branching to penis and integument.

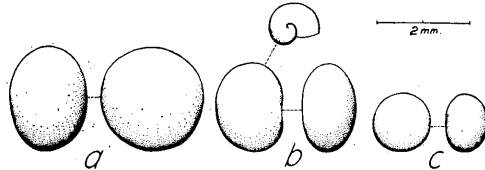


FIGURE 5.—Eggs: a, *Ouagapia ratusukuni*; b, *O. oualanensis*; c, *O. gradata*.

Genitalia (fig. 4, d) on the whole similar to those of above two species, right tentacle free, to left of penis; penis enervated by pedal ganglion. Definitely ovoviviparous: one specimen dissected with egg entire; second (fig. 4, d) with egg shell dissolving and embryo emerging; third with one embryo, no shell fragments. Egg (fig. 5, b) suborbiculate-subrenate, greatest diameter 1.90 mm., height 1.10 mm., one face flatter than the other. Egg shell very delicate, every specimen seen fractured. Embryo (fig. 5, b), greatest diameter 1.10 mm., least 0.90 mm., height 0.50 mm., surface smooth (extracted from egg). Hermaphrodite gland (HG) trilobed, bases of lobes flattened and broad, tapering to efferent ducts. Hermaphrodite duct (HD) convoluted, enlarged at middle. Talon and carrefour (TA; CA) simple. Vas deferens and uterus branching at carrefour but strongly adnate to base of prostate, whence vas deferens (VD) emerges as a convoluted tube which soon straightens. Albumin gland (AG) ovoid, follicles short, erect, numerous. Prostate (Pr) as in others, follicles digitate, lying transversely prostrate, contracted dorsad in gravid individuals (fig. 4, d). Uterus (Ur) narrow above, flared below. Vagina (VAG) proportionately longer than in *O. ratu-*

sukuni or *O. gradata*. Spermatheca (SP) simple short, clavate. Free vas deferens (VD) long, crosses under spermathecal stalk and vagina, around upper atrium and lower penis and empties into epiphallus (EPI) at bulge of penis. Atrium (AT) long, broad. Penis clavate, nearly as long as uterus, stalk broad, apex swollen, epiphallus entering 0.33 of way from below, sheathless. Internally (fig. 4, e) different from above two species, with longitudinal folds on one side, none on the other; large pendent, fist-shaped verge of apex, cleaved longitudinally at epiphallar side, transversely wrinkled. Retractor (PR) apical, large, broad, short, terminating on nuchal membrane.

Caroline Islands: Kusaie, north slope of Mt. Matante (Mt. Buache), alt. 50 to 200 ft., on medium damp dead leaves; 155941 dissected (Micronesian Expedition, Jan. 22, 1936). Mt. Fenkil (Mt. Crozier), alt. about 1,800 ft., on damp dead leaves, Jan. 26, 1936; 156202 dissected; Lele Islet, under dry dead leaves, alt. 354 ft., 155817 dissected.

There are two conchological forms with intergrades of *O. oualanensis* in Kusaie which are usually found together. One is shining above, light colored with few large radiating brown-red zigzag stripes, smooth, without subconcentric malleations, the last whorl rounded (Pease's form); the other is dull above, heavily darkened with numerous thin zigzag stripes, rough, with numerous subconcentric malleations crossing the growth striae, the last whorl slightly flattened above (no. 156113). This latter form, except in size, is close to *O. rapida* Pfeiffer from the New Hebrides which is slightly larger. Pfeiffer (Zeit. Malak. p. 54, 1853) gives the following measurements: whorls 3.5, greatest diam. 7.6 mm., least diam. 6.6 mm., alt. 3 mm. for *O. rapida* and for variety β major, greatest diam. 9.5 mm., least 7.0 mm., and alt. 3.75 mm. Four specimens of *O. rapida* in Bishop Museum (no. 7162) average 8.3 mm. greatest diam., 7.5 mm. least diam., and 3 mm. alt. The average measurements for 5 adult *O. oualanensis* of the form close to *O. rapida* are: whorls 3.5, greatest diam. 6.3 mm., least diam. 5 mm., and alt. 2 mm. A dissection of *O. rapida* may show a close relationship with *O. oualanensis*. They differ principally in size, and both are ovoviviparous.

DISCUSSION

Morphologically, the three species of *Ouagapia* are constructed under identical plans. In all three the organs of the pallial complex are similar, in that the ureter is reflexed and the mantle lappets are three in number and simple. *O. ratusukuni* appears to have the greatest

development, in that it has a covered "secondary ureter." The Kusaiean and Samoan species have only naked furrows (or mere indications of such grooves). The presence of mantle glands in *O. ratusukuni* and *O. gradata* may be of some significance, the importance of which can only be speculated upon at present. In the digestive and nervous systems, and in the external appearance of the animals, no notable differences exist. Except in the number of teeth in each row, the number of rows, and the presence or absence of centrals, the dentition among the three is similar; all the teeth are sharply pointed, are curved, and diminish laterad to triangular marginals. On the female side, the genitalia are nearly identical; hermaphrodite gland saclike, albumin gland compact with numerous follicles, the uterus long, narrow, flaring below with prostate clinging to it nearly its entire length, the spermatheca short. It is only in the penis that some appreciable differences occur, although basically similar, being without any appendix, muscle terminal, and vas deferens emptying into it above the mid-portion. The interior of the *O. ratusukuni* penis is simple, whereas that of *O. gradata* is armed with a rather large stimulator-pilaster, and that of *O. oualanensis* has a large fistlike verge and its vas deferens communicates with the penis by means of an epiphallus.

In reproductive habits, there is definite evidence of ovoviviparity in *O. oualanensis*, whereas both *O. ratusukuni* and *O. gradata* are apparently oviparous. If seasonal collections can be made of these latter two species, their uteri examined, and the above findings confirmed, there may be justification for subgeneric division.

AFFINITIES OF OUAGAPIA

A thorough comparison between *Ouagapia* and related genera cannot be made now for several reasons: (1) there is nothing in available Paryphantidae literature concerning saclike lobes of the hermaphrodite glands, (2) many dissections and observations are incomplete [no mantle organs are described in *Rhenea coresia*, Murdoch (16), although he mentions apparent ovoviviparity while conversely there is no observation on the reproductive habits of *Nata*, Watson (30)], and (3) related species of this genus are unobtainable for dissection at this time. However, *Ouagapia* is related to *Nata* from South Africa and to *Delos* and *Paryphanta* from New Zealand. *Nata* is equipped with two separate mantle lappets (body lobes, Watson) and its kidney has a reflexed ureter. *Ouagapia* is similarly equipped. In genitalia and

teeth the two genera are similar only in a broad sense. The genitalia of *Rhenca* (*Delos*) *coresia* is closer to that of *Ouagapia* in that the oviduct is sacculated and bulges. The prostate is situated on the lower oviduct, spermatheca shortly stalked, free oviduct very short, and the penis simple. It differs from *Ouagapia* only in having a lengthy vagina. For a comparative study of the teeth I have before me Powell's generic types of dentition in Paryphantidae (25, p. 23) and Watson's *Nata* and *Natalina* tooth drawings (30, pl. 19: 4, 9, 10). Because the *Ouagapia* teeth are narrowly based, sharply pointed, considerably curved, and their admedians do not increase abnormally in size laterad, *Rhytida* is eliminated from comparison, leaving *Schizoglossa*, *Wainuia*, *Paryphanta*, *Delos*, *Nata*, and *Natalina*. The base of the ouagapioid tooth comes very close to that of *Delos*. In the admedians being nearly uniform in size, and their gradual diminution toward the marginals, it corresponds most closely to *Paryphanta*. In shape they come closest to *Paryphanta* especially those illustrated by Murdoch: *Paryphanta busbyi* (17, pl. 27: 2, 3), *P. fumosa* (18, pl. 6: 5), *P. atramentaria* (19, pl. 20: 3, 4). They compare well with those illustrated by Hutton: *P. busbyi* (13, pl. 10: 0), *P.* (= *Delos*) *coresia* (pl. 11: E), *P.* (= *Delos*) *jeffreysiana* (pl. 11: F).

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