## On the Locomotion Types of Certain Japanese Gastropods

By

Fumiliro HAYASHI

With 8 Text-figures

(Received December 3, 1936)

### Introduction

It has long been known that various species of gastropods show many different types of locomotion when they creep by means of the rhythmic contraction of the sole musculatures. It was VLÉS (1907) who first classified the peristaltic movement into "direct" and "retrograde" according to whether the waves run from anterior to posterior or from posterior to anterior, and also into "monotaxic," "ditaxic" or "tetrataxic" according to whether the portion of the sole surface traversed by the peristaltic waves is an entire surface, two lateral halves, or four crosswise demarcated sections respec-PARKER (1911) found that there are two subtypes in the "ditaxic" type, namely an "alternate" type, in which the waves in both lateral halves proceed independently (for instance *Tectarius*) and an "opposite" type in which the waves on both lateral halves proceed simultaneously (Nerita). PARKER found also in Illyanassa obsoleta an "arhythmic" type in which the peristaltic waves are indistinct and resemble the gliding movement of the *Planaria*. OLMSTED (1917) reported three new types, the first of which is a "lateral" type with waves traversing the sole from one lateral margin to the other. The second is a "diagonal" type with waves travelling diagonally from the postero-lateral corner to the opposite corner. The third is a "composite" type with both the retrograde and lateral waves appearing at the same time.

Another type of gastropod locomotion not depending upon the peristaltic waves is the so-called "leaping" movement. This was first reported by G. H. PARKER (1922) in *Strombus* and again by H. Weber (1924) in the same genus.

In the spring and summer of 1933 the writer was engaged in studying the locomotion types of Japanese gastropods and recorded those of more than twenty terrestrial and marine species. own examinations included no representatives of the tetrataxic type. but I was able to detect many different subtypes of the diagonal type: direct and retrograde, monotaxic and ditaxic, and, moreover, alternate and opposite among the ditaxic. I also found that the arhythmic type discovered by PARKER may be divided into two: an "uniform gliding" and a "polytaxic contracting" subtype.

Compiling all hitherto known varieties of the locomotion types, gives us the following table. The number attached to some columns denotes the number of Japanese species ascertained by the author.

Rhythmic

A)	Long	gitudinal	
a) Direct			
	i)	Monotaxic14	
	ii)	Ditaxic	
		Alternate 5	
		Opposite	
	iii)	Tetrataxic	
	b) R	etrograde	
	i)	Monotaxic 2	
	ii)	Ditaxic	
		Alternate 9	
		Opposite 1	
	iii)	Tetrataxic	
B)	Diag	onal	
	a) D:	irect	
	i)	Monotaxic	
	ii)	Ditaxic	
		Alternate 3	
		Opposite 1	
	b) Re	etrograde	
	i)	Monotaxic	
	ii)	Ditaxic	
		Alternate 5	
	,_	Opposite	
C)	Later		
	i)	Monotaxic 1	
	ii)	Ditaxic	
	iii)	Tritaxic	

	D)	Composite	
II)	Ar	hythmic	
	· A)	Uniform gliding	15
	B)	Polytaxic contracting	6
III)	Le	ech-like movement	2
IV)	Le	aping movement	1

### Rate of Locomotion

Simultaneous with the study of the locomotion-types, the measurement of the creeping rate was carried on by many investigators, but with no apparent fixed results.

SIMROTH (1879) classified the gastropods into three groups from the character of the sole: "Sohle mit unregelmässige Welle" (Lymnaea), "ganze Sohle mit geordneten Wellen" (Leucochroa, Cepaea, Helix) and "Mittelfeld der Sohle mit geordneten Wellen" (Succinea, Vitrina, Agriolimax, Limax, Arion) and measured the rate of waves in each group.

K. Künkel (1903) called *Arion* "träg und langsam" and *Limax* "mehr oder weniger lebhaft" and classified six species of *Limax* into three groups: "am schnellsten," "weniger lebhaft," and "fast langsam."

G. Bohn (1902) and W. Trappmann (1916) measured the rate of waves in *Helix*, Olshansen (1903) did the same effort by *Arion*, *Limax*, *Agriolimax* and *Helix*, and Parker (1917) by *Aplysia*, Olmsted (1917) by *Cypraea*. But the results obtained by these authors have a diversity that cannot be explained as experimental errors. Perhaps the diversity is due to the presence of some leading factors, internal as well as external, such as the temporary physiological states of individuals, temperature, moisture etc.

The writer endeavoured to register the rate of wave as well as that of creeping in various Japanese gastropods and succeeded with 10 terrestrial and 6 marine species.

### Neuromuscular Mechanism

The third important problem is concerned with the neuromuscular mechanism of the locomotion of the gastropods. Various hypotheses have been published on this problem. The most frequently used materials were pulmonate snails. After some extirpation experiments with *Arion* and *Limax*, KÜNKEL (1903) concluded that the ganglia contained in the nerve nets in the foot-muscles are of sympathetic origin and the peristaltic wave in the sole is automatic in nature. Biedermann (1905) saw that the foot-muscles of *Helix pomatia* can be driven into a tonus state by cutting the pedal nerve which reaches the sole muscle from the pedal ganglion, and was of the opinion that the motor centre of the peristaltic wave in the sole is situated in the pedal ganglion while the pedal nerve net can not display by itself any such peristaltic movements. Biedermann also proposed that the pedal ganglion may act as an inhibitory centre of the tonus as is proved by electrical stimulation of the cut end of the pedal nerve towards the centrifugal direction.

JORDAN (1916) found in *Aplysia* that the extirpation of the cerebral ganglion or the breaking of the cerebro-pedal commissure can induce an increase of tonicity in the isolated portion of the foot. But this did not suggest that the cerebral ganglion is an absolute centre, because a much higher tonicity was obtained by destroying the pedal ganglion. Moreover, such a tonus state in the operated animals was not complete, as they reacted with a further contraction to the electric stimulation applied externally.

Hoping to contribute to the solution of this problem, the present author spent some weeks during the summer of 1933 in carrying on physiological experiments with the neuromuscular mechanism of some Japanese gastropods, of which Euhadra quaesita, Philomycus bilineatus and Agriolimax agrestis varians were excellent materials. Such marine gastropods as Aplysia and Trochus were tried but with poor results. The results obtained during these experiments constitute this paper. While far from satisfactory, it may cast some light on this line of study.

I wish to express my sincerest thanks to Prof. T. KAWAMURA under whose kind supervision this work has been carried on. The identification of the genera and species of the mollusks adopted in this study was done by Mr. T. KURODA of the Geological Institute of the Kyoto Imperial University. I am also indebted in many respects to Mr. I. TAKI of the Marine Biological Station of the Hiroshima Bun-rika University.

## Descriptions of Various Locomotion Types Observed in Japanese Gastropods

### I. Longitudinal type series.

### (1) Monotaxic direct type.

To this belong the following 14 pulmonates:

Euhadra callizona amaliae (KOBELT)*Kuchibeni-maimai
E. herklotsi communis PILSBRYNami-maimai
E. quaesita (DESHAYES)Hidarimaki-maimai
Bradybaena (Acusta) sieboldiana (Pfeiffer)Usukawa-maimai
Plectotropis vulgivaga (SCHMACKER et BOETTGER)Ōke-maimai
Ganesella japonica (Pfeiffer)Nihon-maimai
Bradybaena (Karaftohelix) chishimana (Pilsbry et Hirase)
Karafuto-maimai
Bradybaena similaris (FÉRUSSAC)Onaji-maimai
Trishoplita goodwini (SMITH)Otome-maimai
Phaedusa (Euphaedusa) tau (BOETTGER)Nami-ko-giseru
Dla (Chanach land June) interview (Change)

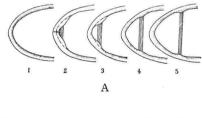
Ph. (Stereophaedusa) japonica (CROSSE).....Nami-giseru Succinea lauta GOULD.....Oka-monoaragai Agriolimax agrestis varians A. ADAMS.....Nohara-namekuji Oncidium verruculatum CUVIER.....Iso-awamochi

In these species the speed of the peristalic wave traversing the sole surface is smaller in the anterior and posterior ends than in the middle portion. The wave length or the antero-posterior extent between two succeeding waves varies also according to the position, being in general largest in the anterior one third of the sole and gradually decreasing in the posterior levels. But the number of waves which the foot exhibits at any moment is fairly constant, a new wave appearing at the posterior end of the foot before the preceding one disappears at the anterior end. In many cases 8 to 12 waves are seen traversing the same sole surface one after another. This number is conveniently denoted as the "wave number" of the species.

Owing to the friction or other hindrances the speed of the foot as a whole does not agree with the speed of the peristaltic waves, even when the direction is common.

<sup>\*</sup> The Japanese name of each species is attached in this column.

Animal	wave distinct or not	wave number	average speed of wave (mm. p. sec.)	average speed of foot (mm. p. sec.)
Euhadra amaliae	distinct	8-9	4.8	0.9
E. communis	distinct	8-9	-	_
E. quaesita	very distinct	10-12	3.9	0.7
Ganesella japonica	indistinct	12-13	5.2	0.7
Bradybaena sieboldiana	distinct	6-8	3.9	1.2
B. chishimana	very indistinct	8		_
B. similaris	indistinct	8-9	2.6	0.6
Trishoplita goodwini	distinct	3-4	_	_
Phaedusa tau	distinct	3	1.9	0.5
Succinea lauta	distinct	3-4	2.5	0.8
Agriolimax agrestis varians	distinct	8-10	3.8	1.7
Oncidium verruculatum	indistinct	2-3	_	_



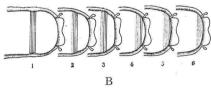


Fig. 1. Progress of peristaltic waves in *Oncidium verculatum*: monotaxic waves appear at the posterior end (A) and disappear in the anterior end (B) of the sole.

I failed in adopting Oncidium verruculatum as material, since it was somewhat out of season at the time of my measurement. But it is a very good material for the demonstration of the monotaxic direct type. However, when using it, it is necessary to use a mirror arranged below a horizontal glass plate, as the animal is not able to stick to the lower side of the glass plate, nor to the vertically set plate.

### (2) Alternate Ditaxic direct type.

This type is represented by the following five aspidobranchiate mollusks:

Monodonta labio (	LINNÉ)Ishidatami
Trochus rota (Du	NKFR)Uzu-ichimonji
	(LINNÉ)Nishiki-uzu
T. tubiferus	(KIENER)Ana-aki-uzu
Haliotis japonica	(Reeve)Tokobushi

Monodonta labio was most frequently used for the experiment. Its wave length is from 3 to 5 mm., the wave number on each lateral half is 2 or 3, often appearing as if 1 or 2, especially so in tiny individuals; but this is due to the fact that the wave is inconspicuous at the beginning or ending. By Trochus tubiferus the wave number is 2-3, the average speed of wave is 4.7 mm. per sec., the average speed of the foot is 2.1 mm. p. sec., the difference in time of the wave progress between the lateral halves is 0.9 second. The wave number in the remaining three species is usually 1, rarely 2.

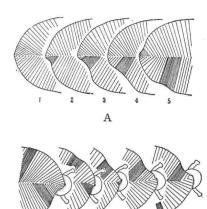


Fig. 2. Alternate progress of peristaltic waves in *Trochus tubiferus*; ditaxic waves of each side appear at the posterior end (A) and disappear at the anterior end (B) of the sole.

### (3) Monotaxic retrograde type.

Two representatives of this type were found:

Cyclophorus herklotsi MARTENS.....Yama-tanishi Tethys dactylomela (RANG)......Janome-amefurashi

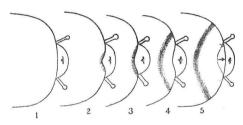


Fig. 3. Monotaxic retrograde wave starting from the anterior end of the sole of *Cyclophorus herklotsi* as the animal proceeds ahead.

In the former the wave is indistinct in the posterior half of the sole. Wave number is 3 or 4, the average speed of the wave 3.8 mm. per sec., the average speed of the foot 0.3 mm. per sec.. In the latter the wave is very distinct, since the zone of contraction occupies a considerably large

area. This zone is narrower in the lateral width than in the other portion. The wave number is 2, the average speed of the wave 10.6 mm. per second, the average speed of the foot 5.1 mm. per second.

### (4) Alternate ditaxic retrograde type.

This is represented by as many as nine of our gastropods, (6 aspidobranchia and 3 pectinibranchia).

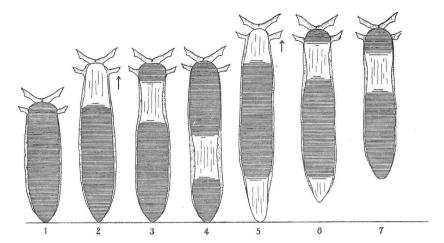


Fig. 4. Monotaxic retrograde waves on the sole of Tethys dactylomela.

Trochus (Tectus) obeliscus GMELINGintakahama
Turbo (Lunella) coronatus coreensis RecluzSugai
Tegula (Chlorostoma) pfeifferi (PHILIPPI)Bateira
Tegula (Chlorostoma) argyrostoma umbilicata (LISCHKE)
Hesoaki-kubogai
Cellana nigrolineata (Reeve)Matsuba-gai
Cellana toreuma (Reeve)Yomegakasa
Littorivaga milegrana (PHILIPPI)Arare-tamakibi
Tectarius vilis (MENKE)Ibo-tamakibi
Astraea (Calcar) haematraga (Menke)ura-uzugai

It is interesting that Trochus obeliscus is retrograde while T. tubiferus is direct as already described. The wave numbers of some of them were measured.

Animals	peristaltic wave distinct or not	wave number	average speed of wave (mm. p. sec.)	average speed of foot (mm. p. sec.)
Trochus obeliscus	very distinct	1-2	-	
Turbo coronatus	distinct in anterior two thirds	1-2	3.4	1.0
Tegula pfeifferi	distinct	1-2		_
T. argyrostoma umbilicata	distinct	1-2		districtly.
Cellana toreuma	indistinct	1-2		
Astraea haematraga	indistinct	1-2		_

### (5) Opposite ditaxic retrograde type.

Our only specimen for this type is *Nerita albicilla* Linné..... (Amaobune). It appears at first glance to be monotaxic, since the median noncontractile zone is inconspicuous. But the contraction zone of the wave shows clearly a bilateral symmetricity, being thinner in the median line than in the lateral margins (fig. 5). Wave number is 1–2; average speed of the wave 7.2 mm. per second, the average speed of the foot 1.2 mm. per second.

### II. Diagonal type series.

### (6) Alternate ditaxic direct type.

Three representatives were found by the writer.

Morula musiva (KIENER).....Reishi-damashi
Thais bronni (DUNKER)....Reishi
Thais clavigera (KÜSTER).....Ibonishi

In the first species, which is an example of this type, the wave-number is 1–2, the average speed of the wave 9.4 mm. p. sec., the average speed of the foot 2.0 mm. p. sec., and the time difference of waves between both lateral halves

is 1.4 sec. The right hand side illustration of fig. 6 was sketched at a moment of the turn to the left.

### (7) Opposite ditaxic direct type.

In *Erosaria* (*Monetaria*) annulus (LINNÉ).....(Hanabira-dakara) both lateral halves of the sole are separated by a thin yellow median line. The wave number is 3–4; the phase on one side fairly agreeing with that on the other side. The average speeds of the wave and the foot are 12.9 and 2.2 mm. p. sec. respectively.

# (8) Alternate ditaxic retrograde Type. To this belong the following only four pectinibranchiate gastropods.

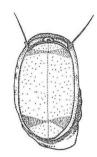


Fig. 5. Opposite ditaxic retrograde waves on the sole of *Nerita albicilla*.

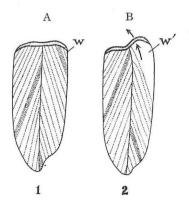


Fig. 6. Morula musiva; A. Diagonal waves proceed towards both antero-lateral corners and disappear at w.; B. At the moment of turning to the right, a modified wave is seen at w'.

apeuthria ferrea (REEVE)Isonina	Japeuthria f
Morula margariticola (BRODERIP)Uné-reishi-damashi	Morula man
Pollia undulata (SCHEPMAN)Shiwa-hora-damashi	Pollia undu
Columbella versicolor SowerbyFutokoro-gai	Columbella

The wave number of the second one is 2, while that of the other four is 1 each. The contour of the sole of the first one recembles that of *Morula musiva*, and agrees with this in being alternate and ditaxic, but differs in being retrograde instead of direct. It is doubtlessly ditaxic, though the median non-contractile zone is inconspicuous. A rippling motion of the anterior margin of the sole is characteristic and is very often seen.

### III. Lateral type series.

### (8) Monotaxic type.

A good example is found in *Erosaria* (*Ravitrona*) caputserpentis (Linné).....(Hanamaru-yuki) in which a peculiar lateral transmission of the peristaltic wave is seen when the animal moves forward. The foot is light yellow in color but the contracted zone is paler. The wave number is 4. A rippling motion is visible at the anterior margin of the foot. A change in the direction of the wave from the right to the left or *vice versa* occurs from time to time, but apparently at no definite intervals.

It is difficult to explain how the forward locomotion is accomplished by such a transverse peristaltic contraction of the sole muscles. I am at present of the opinion that the motion is not forward in a strict sense but is a zigzag course composed of conspicuous diagonal movements.



Fig. 7. Japeuthria ferrea, an alternate ditaxic retrograde wave is visible on the right half of the sole.

### IV. Composite type.

I have never seen gastropods that proceed in the manner reported by OLMSTED, but I am acquainted with certain species which usually depend upon some other types of locomotion and show a composite type at the moment of the turning. Detailed descriptions of them will be given in later pages.

### V. Arhythmic type series.

### (9) Uniform gliding type.

Gliding without any conspicuous peristalsis is a common way of locomotion in gastropods and I can offer the following five pulmonates and ten pectinibranchiate mollusks as representatives of this type.

### (10) Politaxic gliding type.

In this type there is no visible rhythmic wave, but a slight irregular contraction of the sole muscles occurs here and there, while the sole makes a slow forward locomotion. Each portion in which this contraction takes place is generally a narrow zone, though its form differs considerably according to the species, individuals, or the constitution of the ground. A distinct rippling motion is seen at the anterior margin of the foot. The following six pectini-branchiate mollusks may be considered worthy examples.

Chicoreus adustus (LAMARCK)	··Ganzeki-bora
C. elongatus (LAMARCK)	·····Onisazae
Bursa (Tutufa) bufo (Bolten)	··Onaruto-bora
Hemifusus ternatanus (GMELIN)	Tengunishi
Fasciolaria (Pleuroploca) glabra Dunker	····Tsunokigoi
F. (P.) trapezium audouini JonasHin	neitomaki-bora

Of these Bursa is a rather exceptional case, since in it the contraction occurs more or less definitely, i. e. about eight columns

of the gliding zone can be distinguished. There does not seem, however, to exist any connection between these columns.

### VI. Leech-like movement.

This is a rare type in the gastropods, being represented by the following two snails.

Gourmya (Clypeomorus) humilis (DUNKER).....Kayanomi-kanimori Gourmya (Clypeomorus) trailli purpurescens (SOWERBY)......

......Kanetsuke-kanimori

The forward locomotion is achieved by a regular series of motions; the anterior one third of the foot is extended abruptly, the anterior end fixed, and then the remaining parts together with the shell are vigorously pulled forward.

### VII. Leaping movement.

I have seen this type in Strombus (Conomurex) luhuanus LINNÉ. It first supports its body by fixing its claw-like ·····Magaki-gai. operculum at the posterior end of the foot to the substrate and suddenly extends its foot along the entire length so that the body as a whole is thrown out ahead. Then, after fixing the anterior end of the foot, it abruptly shrinks its body longitudinally and leaps a considerable distance. This way of locomotion, therefore, is a modified leech-like movement, being a little more vigorous and covering a wider area than in the above-mentioned cases. Worthy of notice is the fact that an allied species Strombus (Canarium) urceus L.....Mukashitamoto does not leap but merely glides. species also has a claw-like operculum but it is never used for locomotion, except in righting itself. Strombus luhuanus never glides, no matter whether the ground be smooth or rough.

### Change of Locomotion Types

Generally speaking, the locomotion type of the gastropods is definite in each species, but there rarely occur some unusual types. According to Parker (1914), *Chiton*, when vigorously stimulated unilaterally, can make a purely lateral movement apparently by a single wave that sweeps through the foot side-wise. I have seen also some abnormal locomotion types in *Trochus tubiferus* and *T. maculatus*. These are ditaxic-direct in normal forward movement but at the moment of a sudden turn, say to the right, the wave of the right half is abruptly inversed and becomes retrograde. This

is a type that corresponds to the "composite" type of OLMSTED. The same change of wave is also true in the case of *Erosaria* (*Monetaria*) annulus (L.)......Hanabira-dakara.

Erosaria (Ravitrona) caputserpentis (L.)... Hana-maru-yuki, in which the monotaxic lateral is ordinary, becomes ditaxic when the snail attempts to turn to the right or left (Fig. 8, A). If to the right and the wave at that moment is traversing towards the same side, there occurs no change in the anterior half of the sole but the wave is reversed quite suddenly in the posterior half of the sole. Thus the animal rotates its body with the middle portion as a pivot.

If the snail turns to the left while the waves are being directed to the right, the waves in the anterior half are reversed while those in the posterior half retain their direction (Fig. 8, B). At what level the boundary line between these anterior and posterior halves is situated is hard to tell, since this may be shifted considerably but it is always within the middle one third of the sole, never appearing closer to the anterior or the posterior end.

Erosaria annulus is also a remarkable example of the changeable type. This species is ditaxic-direct in its ordinary forward locomotion but becomes a lateral type when turning. The change is quite abrupt, the direct wave being given up suddenly and lateral waves starting from one side. Thus E. annulus agrees with E. caput-serpentes in that the turning is done by means of lateral waves but differs from it in that the posterior half of the sole does not show any reversal of the waves at all.

PARKER (1914) and OLMSTED (1917) have noticed the backward

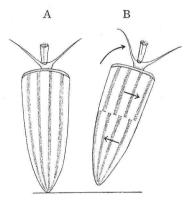


Fig. 8. *Erosaria caputserpentis* in ordinary progress (A) and in left side turn (B). See lateral waves and their change of direction.

motion in *Chiton* and *Fissurella*. I have observed the same motion in our *Trochus tubiferus* and *T. maculatus*. When stimulated at the anterior end of the foot by stinging with a small needle, these gastropods stop first and then begin to creep backward by starting a monotaxic retrograde wave, of which the wave number is 1, and stop again when this wave has traversed the entire length of the foot. If one more stimulus is given, the animal retires just as long

as a new single wave is going on. If such stimulation is repeated four or five times the animal begins to retrograde intentionally and continues this for a few minutes. It is noticeable that our *Trochus* is ditaxic-direct in the nomal forward motion and becomes monotaxic retrograde in the backward motion. In this respect the genus differs from *Chiton* and *Fissurella*, which are always of a retrograde type, either in the forward or the backward motion.

## The Neuromuscular Mechanism of the Pedal Locomotions in Some Gastropods

The paralyzing of the snail is achieved by first dipping the animal into warm water (30-35 °C) until the animal extends its soft parts out of the shell and then gradually adding 70 % alcohol until the solution becomes 1.75 % concentrated. In half an hour the snail becomes almost senseless and does not react to a needle prick. A similar state can be reached in only a few minutes by narcotising the animal with cocain injection. About 0.1-0.2 cc. of 2% cocain solution is sufficient to paralyse a full grown Euhadra and 0.03cc. of the same for Acusta. The injection needle is better thrust toward the head end, since this prevents the head from withdrawing into the shell and at the same time permits the needle to go deeper into the body. The drawback to the cocain method is in the difficulty of finding suitable dose of cocain. If too much is administered, the animal soon perishes, while if too little the animal contracts and dies of bleeding. The warm water method is best because the mortality rate is lowest, provided that it is convenient to operate on the animal quickly in order to cut the nerve fibers.

The nerve fibres were usually broken by means of a small pair of scissors or sometimes with a small hook-shaped needle. A ligature with a thin silk thread and burning by electrically heated wire were methods employed in some experiments.

In the following pulmonates a distinct tonus was observed in the isolated portion of the foot and it was again released by stimulating electrically the centrifugal nerve fibres.

Euhadra callizona amaliae (KOBELT) E. herklotsi communis PILSBRY Acusta sieboldiana (PFEIFFER) Ganesella japonica (PFEIFFER) In *Philomycus bilineatus* Benson and *Agriolimax agrestis varians* A. Adams, the pedal musculature does not show any tonicity after the breaking of the pedal nerve. Even after the body of *Philomycus* is divided by a transverse cut into two halves, both the anterior and posterior portions continue their creeping movement for some time. Then the posterior portion begins to diminish its speed earlier than the anterior, till at last the rate of the posterior portion corresponds to about 1/10 of the anterior.

The same experiment can be performed with *A. agrestis varians*, but in this species both halves can proceed much more quickly than those of *Philomycus*. In short, the pedal musculature of the two Japanese species of slug can not be brought to a complete tonicity by destroying its pedal ganglion.

The same operation was tried with *Tethys dactylomela* and could cause a typical tonus state, but this was a little weaker than in the case of *Euhadra* or *Acusta*. A somewhat similar result was obtained in experiments with *Trochus tubiferus*.

#### Literature

- Biedermann, W. 1905. Studien zur vergleichenden Physiologie der Peristaltischen Bewegungen. II. Die lokomotorische Wellen der Schneckensohle: Pflüg. Archiv, Bd. 107, S. 1-56.
- —— 1906. Dieselbe. III. Die Innervation der Schneckensohle: Ibid. Bd. 111, S. 251-297.
- CAR, L. 1897. Mechanismus der Lokomotion bei den Pulmonaten: Biol. Centralbl., Bd. 17, S. 426-438.
- Carlson, A. J. 1905. The physiology of locomotion in Gastropods: Biol. Bull., Vol. 8, p. 85-92.
- Fröhlich, F. W. 1910. Experimentelle Studien am Nervensystem der Mollusken. IX. Das Sauerstoffbedürfnis des Nervensystems von *Aplysia limacina*: Zeitschr. f. allg. Physiol. Bd. 11, S. 121-140.
- —— 1910 a. Dieselbe. XII. Summation, "scheinbare Bahnung," Tonus, Hemmung und Rhythmus am Nervensystem von *Aplysia limacina*: Ibid., Bd. 11, S. 275-316.
- —— 1910 b. Dieselbe. XIII. Ueber die durch das Pedalganglion von *Aplysia limacina* vermittelte Reflexkettung: Ibid., Bd. 11, S. 351-370.
- JORDAN, H. 1901. Die Physiologie der Locomotion bei Aplysia limacina: Zeits. f. Biol. Bd. 41, S. 196-238.
- —— 1905 a. The physiology of locomotion in Gastropods; A reply to A. J. Carlson: Biol. Bull., Vol. 9, p. 138-140.
- 1905 b. Untersuchungen zur Physiologie des Nervensystems bei Pulmonaten.
   I: Pflügers Arch. f. ges. Physiol. Bd. 106, S. 189-228.
- --- 1905 c. Dieselbe. II: Ibid., Bd. 110, S. 533-597.
- —— 1916. Können gesteigerter Widerstand gegen Ausdehnung sowie Tonuszunahme nach Extirpation der Pedalganglion bei *Aphysia* durch "scheinbare Erregbarkeitssteigerung" erklärt werden? Zeits. f. all. Physiol. Bd. 17, S. 146-163.

- JORDAN, H. und P. J. VAN DER FEEN jun. 1929. Methoden und Technik der Nerven und Muskelphysiologie bei wirbellosen Tieren: Handb. d. biol. Arbeitsmethoden, Heft 3, S. 357-372.
- Künkel, K. 1903. Zur Locomotion unserer Nacktschnecken: Zool. Anz., Bd. 26, S. 560-566.
- OLMSTED, J. M. D. 1917. Notes on the Locomotion of certain Bermudian Mollusks: Jour. Exp. Zool., Vol. 24, pp. 221-236.
- PARKER G. H. 1917. The mechanism of locomotion in gastropods: Jour. of Morph. Vol. 22.
- --- 1914. The locomotion of Chiton: Contrib. Bermuda Biol. Sta., No. 31, pp. 1-2.
- —— 1917. The pedal locomotion of the sea-hare Aplysia californica: Jour. Exp. Zool., Vol. 24, pp. 139-145.
- —— 1922. The leaping of the stromb (Strombus gigas Linn.): Jour. Exper. Zool., Vol. 36, No. 2.
- Simroth, H. 1878. Die Tätigkeit der willkürlichen Muskulatur unserer Landschnecken Zeits. f. wiss. Zool., Bd. 30, Suppl. S. 166-224.
- --- 1879. Die Bewegung unserer Landschnecken, hauptsächlich erörtert an der Sohle des *Limax cinereoniger* Wolf: Zeits. f. wiss. Zool., Bd. 32, S. 284-322.
- VLÉS, F. 1907. Sur les ondes pedienses des Mollusques reputateurs: Compt. rend. Acad. Sci., Paris, tome 145, p. 276-278.
- Weber, H. 1924. Ueber arhythmische Fortbewegung bei einigen Prosobranchiern: Zeits. f. vergl. Physiol., Bd. 2 S. 109-121.