

**THE EVOLUTION OF ARTHROPODAN LOCOMOTORY MECHANISMS.—
PART 4. THE STRUCTURE, HABITS AND EVOLUTION OF THE
DIPLOPODA.** By S. M. MANTON, F.R.S., from the Zoological Department
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(PLATES 52–55, and 8 text-figures.)

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CONTENTS.

	Page
Introduction	300
Methods	302
Movements of the head and body	303
Inter-ring joints and ring morphology	304
Skeleto-muscular system of the Juliformia	306
Movements between the rings	310
Dorso-ventral bending	311
Rotation between the rings along the long axis of the body	312
Skeleto-muscular system of the Polydesmoidea	312
Skeleto-muscular system of the Oniscomorpha	315
Skeleto-muscular system of the Nematophora	321
Skeleto-muscular system of the Colobognatha	323
Structures permitting the spiral position	324
The collum and keels and the ability to push	325
Skeletal and muscular systems	327
The manner of discharge of the stink glands	328
General character of the gaits	328
Variations in the locomotory movements	331
The pattern of the gaits and the phase differences between successive legs	331
The angle of swing of the leg	334
The constancy of the forward stroke	335
Pace duration	336
Speed	336
Locomotory movements of the sternites	338
Pushing power	340
Effect of legs of different types, and of the heaviness of build of the body, on pushing power, speed and habits	341
Effect of ring size on pushing power	343
Effects of ring shape and ring number on pushing power	345
The evolution of the diplo-segment	348
The nature of the apparently single anterior segments and the locomotion of the early instars	349
Morphological features associated with locomotory habits	352
Pushing and rolling up	352
Rock-climbing	353
The evolution of the Diplopoda	356
Primitive and specialized features, the Colobognatha and Oniscomorpha	356
Primitive millipedes	358
Juliformia	359
Polydesmoidea	359
Nematophora	360
Conclusions	363
Summary	365
Acknowledgments	366
References	366
Description of Plates	367

INTRODUCTION.

Brief descriptions of the metachronal waves of limb movement shown by millipedes are to be found in the works of Clementi (1912), Bethe & Salmonson (1931), Bethe & Thorner (1933), Holst (1934 and 1935) and others, besides the larger monographs on the Diplopoda. Lankester (1904) made careful and accurate observations on the juliform *Archistreptus*, and noted that the phenomena of millipede limbs can be studied satisfactorily only by photography and "the instantaneous illumination of the electric spark". The results of such a study are presented below. The main theme of the more detailed earlier investigations on millipede locomotion has been the mode of co-ordination of the movements and the physiology of the spiral reflex, and not the function of the various types of movements. Alterations in some features of the metachronal waves have been obtained from experimental methods involving partial destruction of the animal, but details of the normal range of locomotory performances by millipedes have not yet been previously ascertained, nor have the far reaching correlations of structure with habits been appreciated. The data presented here provide functional reasons for the evolution of many of the diagnostic characters of the trunk region of the Diplopoda as a whole and of its several sub-divisions.

In Part 3 it was shown how (a) the chilopodan locomotory mechanisms appear to be specialized derivatives of two primitive gaits such as seen in Peripatus (the 'middle' and 'top-gear' gaits, see Part 1) and (b) the view was put forward that many diagnostic features of the chilopodan groups have been evolved in association with persistent habits, those concerning a striving after speed or a perfection of burrowing being the more important. Here it will be shown how a 'bottom-gear' gait, such as seen in Peripatus, has been exploited by the Diplopoda, and how diagnostic features of this group have probably also evolved in association with persistent habits. A tendency by ancestral Diplopoda to push through and into the substratum by the motive force of their legs appears to have been of basic importance, in contrast to one of running round obstacles as practised by the Chilopoda. The resultant method of burrowing in Diplopoda is quite unlike that of the burrowing Chilopoda (Geophilomorpha, see Part 3).

Arthropodan advances concerning rigidity of integument, joints, length of the leg, form or the limb-tip and the hanging stance were necessary preliminaries for the evolution of diplopodan locomotory mechanisms (see Part 2, pp. 96, 97, etc), and a common origin of diplopod and chilopod gaits cannot be envisaged at a stage much less distant than that of a soft bodied arthropod (see Part 2, p. 115 and below).

The diplopodan groups are varied both in their general appearance and habits of life but, as pointed out by Attems (1926) and others, the majority live under decaying leaves and in the underlying humus of woodlands. Most Diplopoda are herbivorous, feeding on fresh or decaying vegetable matter, a few are omnivorous, taking also earthworms, phalangids and insects, some are scavengers and a few are carnivorous (Attems, 1926; Verhoeff, 1926-32; and Brade-Birks, 1930). Usually diplopods do not wander far from their place of birth, and an ability to run fast appears to be an incidental rather than an essential accomplishment, although speed may sometimes be important, particularly to the larger species.

A marked ability to push is as diagnostic of the Diplopoda as is the possession of diplo-segments. This, and the ability to curl the body into a tight or a loose spiral, are two habits which must have been of major importance in the evolution of the structural peculiarities of the group. The Chilopoda and the smaller myriapodan groups are not capable of much pushing. The ability to push is exercised in different ways. The Juliformia and Oniscomorpha employ bulldozer-like tactics, pushing mainly by the head end in penetrating soil, and the anterior end of their bodies is almost as wide as any other part. The British Polydesmoidea and Nematophora cannot penetrate so deeply, being found in woodland litter, and specialize in forcing open cracks which tend to give way along one plane, the force being applied by their 'flat backs'. In the Nematophora and in *Polyzonium* the body markedly tapers anteriorly, assisting the animal to transfer a forward thrust to the dorsal surface.

In all cases the legs supply the motive force, but in the Nematophora, Oniscomorpha and Colobognatha longitudinal and oblique muscles, which slide the sternites and leg bases antero-posteriorly, also contribute to the locomotory thrust. The presence of free sliding sternites in these three groups also makes possible a tight spiral position, as well as serving locomotory needs. In the Juliformia and Polydesmoidea the pushing power of the legs is developed from rigid leg bases, and this has brought problems in effecting a close spiral, solved to different degrees and by different means in the two groups.

In the taxonomic literature, little of which is in English, some skeletal parts of millipedes are described in detail, but the correlations which can be shown to exist between skeleto-muscular systems, function and habits have scarcely been appreciated. The purpose of the short descriptions of skeleto-muscular systems given here is not to add to taxonomic knowledge nor to describe the various structures fully, but to interpret structure in terms of function in a manner serviceable to the non-specialist.

The representative animals of the major groups of Diplopoda which have been studied, on the classification adopted by Attems (1926), are listed below, and those which have not been obtained alive are bracketed.

Opisthandria		
	Limacomorpha	(<i>Glomeridesmus mexicanus</i>)
	Oniscomorpha	(<i>Sphaerotherium dorsale</i>)
		(<i>Sphaerotherium giganteum</i>)
		(<i>Glomeris marginata</i>)
Proterandria		
Eugnatha		
	Polydesmoidea	<i>Polydesmus coriaceus</i> <i>Polydesmus angustus</i> <i>Brachydesmus superus</i> (<i>Oniscodesmus fuhrmanni</i>) <i>Microchordeuma (Chordeumella)</i> <i>scutellare</i> var. <i>brölemanni</i>
Nematophora		
	Chordeumoidea	<i>Craspedosoma rawlinsi</i> <i>Polymicrodon polydesmoides</i> (<i>Callipus foetidissimus</i>) (<i>Lysiopetalum illyricum</i>)
Juliformia		
	Juloidea	<i>Blaniulus guttulatus</i> <i>Cylindroiulus punctatus</i> <i>Cylindroiulus londinensis</i> var. <i>caeruleocinctus</i> <i>Schizophyllum sabulosum</i> <i>Micropodoiulus scandinavius</i> <i>Tachypodoiulus niger</i> <i>Graphidostreptus judaicus</i> (<i>Gymnostreptus tabulinus</i>) <i>Plusioporus sulcatus</i> (<i>Poratophilus punctatus</i>) <i>Ophistreptus guineensis</i> (unidentified species) <i>Polyzonium germanicum</i>
Colobognatha		
	Spirostreptomorpha	
	Spiroboloidea	

Silvestri (1903), Verhoeff (1926–32), Attems (1926) and Brölemann (1935) have each used a different terminology for the leg segments of the Diplopoda. The naming of the segments adopted here for a six-segmented leg is : (1) coxa, (2) prefemur,

(3) femur, (4) postfemur, (5) tibia and (6) tarsus. The term trochanter is used for an additional segment situated in between (1) and (2), and tarsus 1 and tarsus 2 for segments resulting from an incomplete division of the tarsus. The muscle of the tarsal claw is referred to as the flexor unguiculi.

The terminology used for the muscles is based on that of Silvestri (1903), modified in accordance with the naming of the limb segments here adopted.

The locomotory mechanisms of the Pselaphognatha will be considered in Part 5.

METHODS.

When given a smooth substratum exposed to daylight, Diplopoda do not readily perform a wide range of gaits at very different speeds, as do many Chilopoda, Arachnida and Insecta. Some species may not alter the gait at all (see entry for *Polydesmus* in Table 1, Part 2, p. 104) and merely change the speed a little by alterations in the pace duration and angle of swing of the leg. Under such conditions millipedes exhibit their faster gaits, and these are usually of lesser significance to the animals than their slower gaits. It is necessary to supply some resistance to an animal's progression in order to call forth the wide range of gaits of which it is capable, and in particular the slow powerful gaits which, it is suggested here, have been of major significance in the evolution of the group.

It has not been practicable to record behaviour while burrowing or pushing under natural cover, but millipedes have been harnessed to sledges, which they pull with great readiness. The more powerful gaits are employed as the load is increased, and the maximum load which can steadily be drawn has been ascertained. The Onychophora and Chilopoda when harnessed make no attempt to pull a load by the motive force of their legs.

Flat bottomed pans of appropriate sizes have been used as sledges, the contained loads being easily changed. The harness has consisted of threads of appropriate thickness temporarily stuck to the whole length of the millipede by means of 'Noso', a quick setting preparation which can later be peeled off without damage to the animal. For large species, the harness is most easily secured beneath a strip of cotton or silk material, the whole length of which is stuck to the exoskeleton. Millipedes have also been saddled with weights (see Pl. 52, figs. 12-14), but it is usually more difficult to apply a maximum load by this means; the animals again appear quite 'complacent' and exhibit gaits appropriate to the loads. The maximum load which each animal can pull steadily has been recorded in terms of the force in grams required similarly to shift the sledge and harness. The method is subject to obvious inaccuracies, but it is nevertheless of value for comparative purposes, and it gives reasonably consistent results within the same species.

Owing to the large number of legs possessed by many millipedes it has been desirable in some cases to apply a 'boot' of some quick-setting plastic material to one foot in order to ascertain the stride length from tracks made by the animal walking over smoked paper. The general methods employed have been described in Part 2. Some of the photographs shown on the plates, in which all legs are sharp, were taken with electronic flash illumination; the procedure of adopting an exposure time which will give a blurred image of the legs performing the recovery stroke is less useful for millipedes than it is for centipedes.

A ventral view of moving limbs and sternal plates can easily be obtained by allowing an animal to walk across one-half of the long face of a right-angled prism and focussing a binocular microscope on the inverted image visible on the other half of the long face. Photography is, however, needed for the analysis of these movements, and for this purpose the animals have been photographed from below when walking across cover glass. Loading the animals under such conditions cannot be carried far because their feet slip on the glass.

MOVEMENTS OF THE HEAD AND BODY AND OCCURRENCE OF UNDULATIONS.

Lateral movements of the head during walking, which have been described for the Onychophora and Chilopoda (Parts 1 and 3) are also seen in a more limited degree in many Diplopoda. There is less movement of the head relative to the trunk, the anterior segments contribute to the bending (Pls. 53, 54, 55, figs. 23, 24 and 37–41), and the antennae touch the ground momentarily, as in other Myriapoda. The two antennae may be put down together, or they may tap the ground alternately as is so often done by *Glomeris*.

The conspicuous changes in length and shape of the body seen in the Onychophora and Chilopoda are absent in most Diplopoda. Effective burrowing could not be achieved by a bulldozer method if the rings of the body readily telescoped or altered in shape. The apparent length of *Ophistreptus guineensis* when walking freely, when walking against a drag applied to the posterior end, or when walking against a resistance applied at the head end is almost the same, changing by about 1 per cent, in contrast to the Onychophora and Geophilomorpha, whose shape changes greatly under different circumstances, increasing up to 60 per cent in length (Parts 1 and 3). *Polydesmus* also maintains an almost constant length. Other Juliformia which have been examined can alter their length by 2–5 per cent, the amount differing in the several species. The longer dimensions are usually but not always associated with the faster gaits. *Craspedosoma* can increase its walking length by 5 per cent, the shorter lengths being seen when the animal is progressing against a resistance, as in Pl. 53, fig. 21, where the length of the body, including the hump, is less than in the freely walking animal in fig. 20. The length of *Glomeris*, excluding the head and collum, which can be considerably extended, may differ by 10 per cent at different moments, but the extension of the body does not appear to be uniformly related to the gait. Possibly this may be due to constant changes in behaviour under experimental conditions. *Polyzonium* when walking fast may be 17 per cent longer than it is when pulling a load, but in Pl. 55, fig. 48 it is only a little over 3 per cent longer than it is in fig. 49. However, in this millipede the extensibility of the body is probably necessary in order that a flattened form may be assumed when hanging on to rock in a chiton-like manner (p. 353).

A push can be exerted by the head end of a juliform millipede when the body is held in any position and even as in text-fig. 1 c, although a force can most easily be applied when the body is straight. For this it is essential that each ring should maintain its position rigidly, relative to the next. Immovable objects, such as stones, encountered in burrowing can thus be avoided and the most favourable path followed. Text-fig. 1 c shows an *Ophistreptus guineensis* walking between a series of pegs. The flexibility of the millipede body, particularly in the Juliformia, is as striking as is the ability to hold the rings firmly in any position.

The power to rotate one ring upon the next is also conspicuous. A minor use of this ability is seen when an animal walks away from a spiral stance on a flat surface; the anterior rings then lie at right angles to those still in the spiral. The maximum powers of rotation are not easy to elicit. An *Ophistreptus guineensis* has been observed to rotate one ring upon another by 11° or more. If the two ends of the body are held as indicated in text-fig. 1 b, so that the animal cannot walk away, the legs of the middle rings may leave the ground and be carried round laterally, than dorsally, and even over to the other side through an angle of 270°. It is not known whether such rotation is used in burrowing to bring the legs in contact with the most favourable footholds. Since such great powers of rotation have no obvious purpose in surface walking, the existence of these powers suggests that they may be of service in burrowing. Millipedes which burrow less well, such as the Polydesmoidea, have not been observed to rotate their rings so greatly.

Undulations of the body, which are usually undesirable in the Arthropoda (Part 2, p. 113), are seldom conspicuous in freely walking Diplopoda, being controlled by the strong inter-ring musculature, which is needed to maintain or modify any

given flexure when the animal is pushing with the legs. The mid-ventral origin of the legs and each pair being moved in the same phase may give a tendency towards dorsal humping over the groups of propulsive legs, comparable with the lateral undulations of centipedes (Parts 2 and 3), but such undulations are never apparent. An inability to control body undulations does not arise in the Diplopoda as in the Chilopoda, and does not provide a limiting factor for the exploitation of the type of gait employed. Dorsal humping over the groups of legs in the recovery phase may be seen in animals which are exerting themselves, either by running fast or by pushing against a resistance, but this is an active locomotory movement (see p. 339).

The changes in shape undergone by a ring in the Oniscomorpha and Colobognatha are considered on pp. 315 and 323.

Some species of Juliformia can on occasion move about by body wriggling without the legs. Duncan (1897) records African Juliformia turning on their backs and retreating without using the legs, and the same phenomenon has been seen in this country in *Tachypodoiulus* (Cloudsley-Thompson, 1949) and other species. This capacity is serviceable in making a way through grass, but no evidence has been obtained of a widespread utilization of such a method of progression. When juliform millipedes were caused to progress between a series of pegs, as in text-fig. 1c, in all cases the legs alone were used, either against the ground or against the pegs, and the animals did not appear to progress by pressing against the pegs with the body. A snake-like wriggling appears to be an incidental accomplishment, and not a habit that has been of importance in the evolution of the Diplopoda, where the usual method of walking and burrowing appears to be mediated by a force exerted through the legs.

The movements occurring between the body rings of millipedes, and the skeleto-muscular systems which make these movements possible, will be described in outline before the locomotory mechanisms are considered.

INTER-RING JOINTS AND RING MORPHOLOGY.

The ability to push by the head end or dorsal surface is correlated in all groups of Diplopoda with a very strong exoskeleton. The mobility of one ring upon another is great, allowing a general flexibility of the body which in some groups is striking. Each ring is united with the next by a long thin flexible membrane (text-fig. 3, *i.m.*) which may be up to half the length of a ring. This membrane arises from the outer side of the prophragma or from the anterior end of a ring. It folds forwards and then backwards, to unite with the underside of the metazonite, a considerable distance anterior to the free margin (text-fig. 3, *o.i.m.*). The rings of the Juliformia can be pulled out to double their original length if the muscles are removed, but in life the rings of one part of the animal can be artificially pulled out only to a length 7 per cent greater than normal ; but so great an extension does not take place under usual circumstances. If forces directed towards each other are applied at two points on the body of a living juliform millipede, little, if any, shortening of the intervening rings results. In all groups of millipedes structures exist which prevent the telescoping of one ring into the next when pressure is applied or when the animals push.

Most descriptions of the inter-ring joints of millipedes have stressed their telescopic overlapping, and Attems' (1926, fig. 51) scheme for the joint movements of a julid shows what amounts to a ventral hinge, and if the diagrams were extended, they could never truly represent a straight animal. Brölemann (1935) correctly notes that the axis of rotation of the inter-ring joint lies half-way up the side, but he reproduces Attems' figures. A ball and socket joint, or a derivative of this type, has been found in all millipedes used for the present investigation.

Both skeleton and muscles prevent the 'ball' from sinking deeper into the 'socket'. That the 'ball' is loosely held in place by muscles is shown by the lengths of dead Polydesmoidea and Juliformia being slightly less than in life. The skeletal joints in these two groups are incompressible and prevent further shortening. In the Nematophora and Oniscomorpha the ring skeleton is not fused into one piece as in the former groups, and it is not so rigid. In life muscles keep the 'ball' in position, since length changes in life are small (see above, p. 303), while a 40 per cent shortening may occur on death in *Craspedosoma* for example. Displacement of the 'ball' on one side, laterally, ventrally or dorsally is accompanied by an equal and opposite displacement on the other side. There is no telescoping in the sense that one hard part slips a variable distance into a sleeve of another hard part, except to a very small extent in the Nematophora, Oniscomorpha and Colobognatha. A millipede may be likened to a series of opisthocelous vertebrae which have been drilled out down the middle to house the viscera, each part being fashioned like a beautiful piece of machinery.

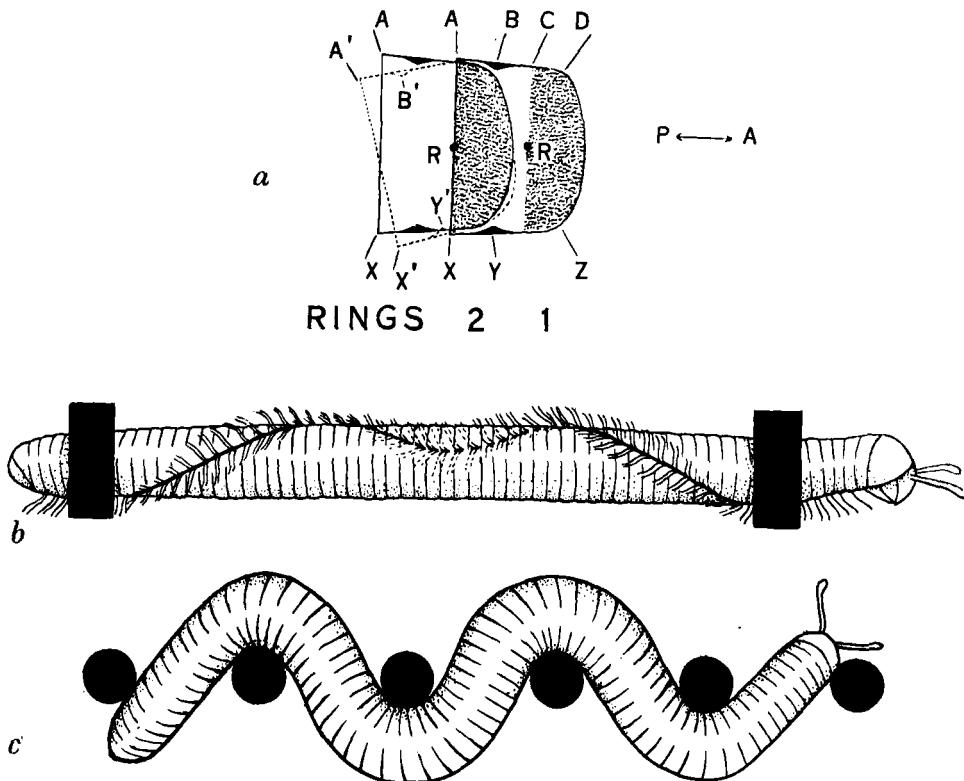
In the Polydesmoidea (*Polydesmus*, text-figs. 2 e-i) and in the Nematophora (*Polymicrodon*, text-figs. 2 o and p) the ball and socket is very simple. The anterior end of the prozonite tapers steeply, ending in a thickened strengthening rim, and is inserted into a widening funnel provided by the metazonite of the preceding ring. The free edge of the metazonite is also strengthened by thickening on its inner margin and can resist deformatory tendencies. The extent of the 'ball' is shown by the mechanically tinted regions in text-fig. 2, this being the part of the prozonite which is covered by the metazonite of the preceding ring when the body is straight. The incompleteness ventrally of the 'einschubcylinder' of *Polymicrodon* presents little difference functionally from *Polydesmus*, since the parts concerned act as a ball and socket in the absence of complete ventral continuity of the socket, which is otherwise circular in section. In the Juliformia the overlapping parts taper, but less steeply in the larger species, and the joint is more elaborate, allowing wider movements, particularly those which permit the spiral reflex.

Some essential features of the joint and its movements are shown by text-fig. 1 a. Ring 2 fits into ring 1 as shown, the tinted part forming the 'ball' being covered when the animal is straight. This ring is deeper and shorter than it is in the Polydesmoidea, Nematophora Chordeumoidea, and less deep than is usual in the Juliformia and Lysiopetaloidae. The most anterior part of the prozonite, midway between D and Z, reaches just beyond the supposed junction of pro- and metazonite at B-Y, as in the Juliformia. This junction is marked by a diagrammatic thickening (black), but in the Polydesmoidea, Nematophora, Juliformia and Colobognatha a constriction or furrow lies in this position (see B on text-figs. 2, 3 and 4, and Pls. 52, 53, 54, 55, figs. 11, 25, 26, 37 and 44). This furrow in the latter two orders resists the telescoping of one ring into the next, while in the longer ringed Polydesmoidea and Nematomorpha the tapering shape of the 'ball' and 'socket' prevents the 'ball' from reaching this middle level of the ring.

If ring 2 in text-fig. 1 a is rotated about the centre R midway between A and X, so that its anterior end turns upwards, the rotation will be stopped by mechanical interference of the margin X of ring 1, as is shown by the dotted line. If a constriction lay around the ring between B¹ and Y¹, the rotation could be carried a little farther, since the rim X of ring 1 would slip into the furrow at Y¹. Further, rings proportioned so as to give smaller distances A-B and X-Y (shorter deeper rings) will possess a smaller angle of rotation of one ring upon the next. The formation of a resistant socket necessitates the greater part of the exoskeleton being in the form of one rigid unit.

The limbs of all Diplopoda can exert a powerful push, and for this the extrinsic muscles need suitably placed firm sites for their insertions. In the Juliformia and Polydesmoidea the legs articulate with rigid sternites immovably fixed to the terga, and extrinsic leg muscles are inserted on to the equally firm tracheal pouches. In the

Oniscomorpha, Nematophora and Colobognatha where the sternites and associated tracheal pouches are free, there is an abundance of muscles to the tracheal pouches which slide these structures, and indirectly the bases of the legs, posteriorly during the backstroke and forwards during the recovery stroke (see p. 338), thus assisting the extrinsic leg muscles in supplying a propulsive force. These muscles must also provide rigidity.

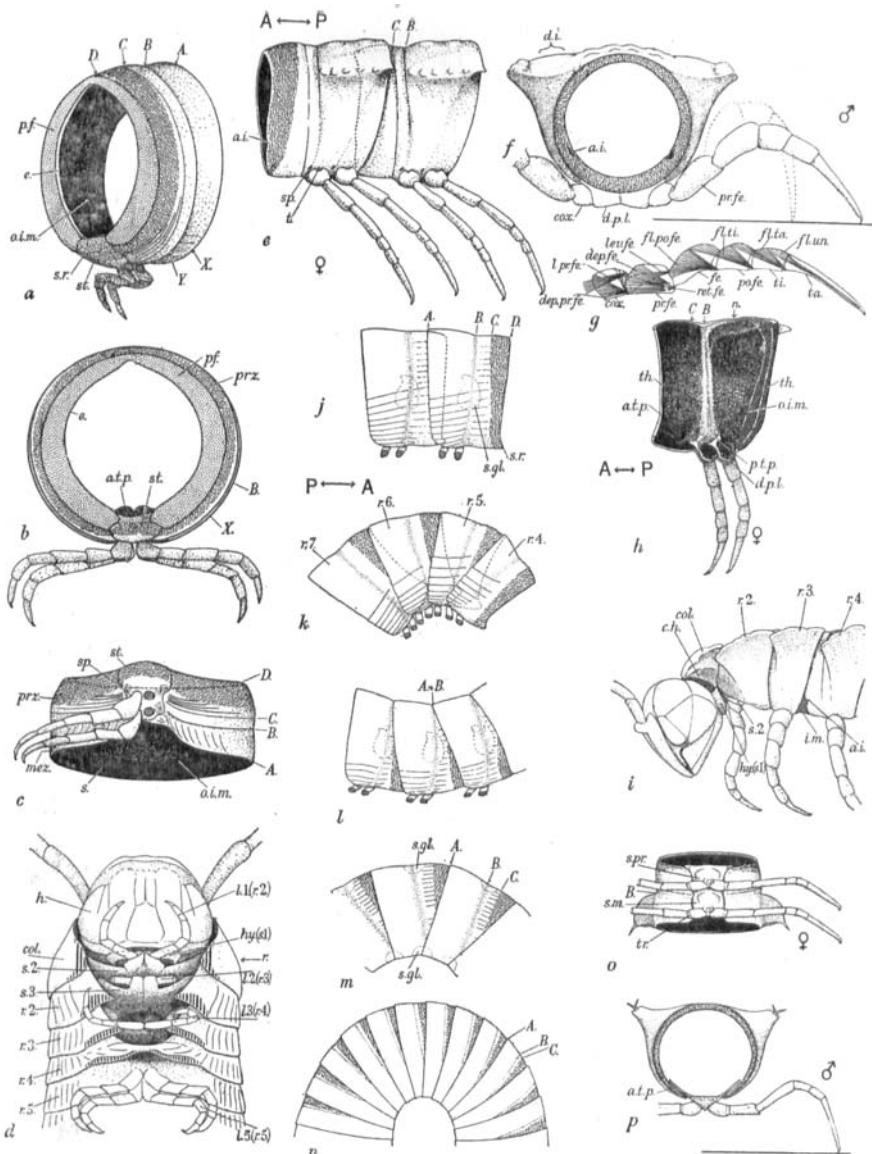


TEXT-FIG. 1.

- (a) Diagram of two rings of a millipede to show the ball and socket joint between them.
- (b) *Ophistreptus guineensis* showing rotation of the rings following on the body being held by the clamps as shown.
- (c) *O. guineensis* walking between a row of pegs (the size of the pegs corresponds to that of an ordinary pin relative to *Blaniulus guttulatus*).

SKELETO-MUSCULAR SYSTEM OF THE JULIFORMIA.

The exoskeleton of a ring of *Gymnostreptus* is shown in text-figs. 2 a-c. The sternites and tergites are fused, the 'ball' D-C fits into the metazonite socket A-B and the 'ball' tapers anteriorly. The constriction B lies parallel to the anterior end of the ring, which is much shorter ventrally than dorsally. The posterior margin A-X slopes towards the constriction B in the latero-ventral direction. The limit C of the normal dorsal overlap of the rings when the body is straight is in many species marked either by a line of some kind or by different sculpturing on either side of this line. The mark C continues round the sides of the ring parallel to the anterior margin (see also the Polydesmoidea, text-fig. 2 e). The short sternal region is emarginated posteriorly and projects anteriorly beyond the



TEXT-FIG. 2.

Diagrams illustrating the skeleton of millipedes, the extent of flexures between the rings and the form and positions of the legs. Prophragma mechanically stippled, portion of outer surface of prozonite covered by preceding ring when the body is straight is mechanically shaded. For key to lettering see text-fig. 3.

(a-c) Ring skeleton of *Gynostreptus tabulinus* (Juliformia), (a) in oblique lateral view, (b) in anterior view and (c) in ventral view.

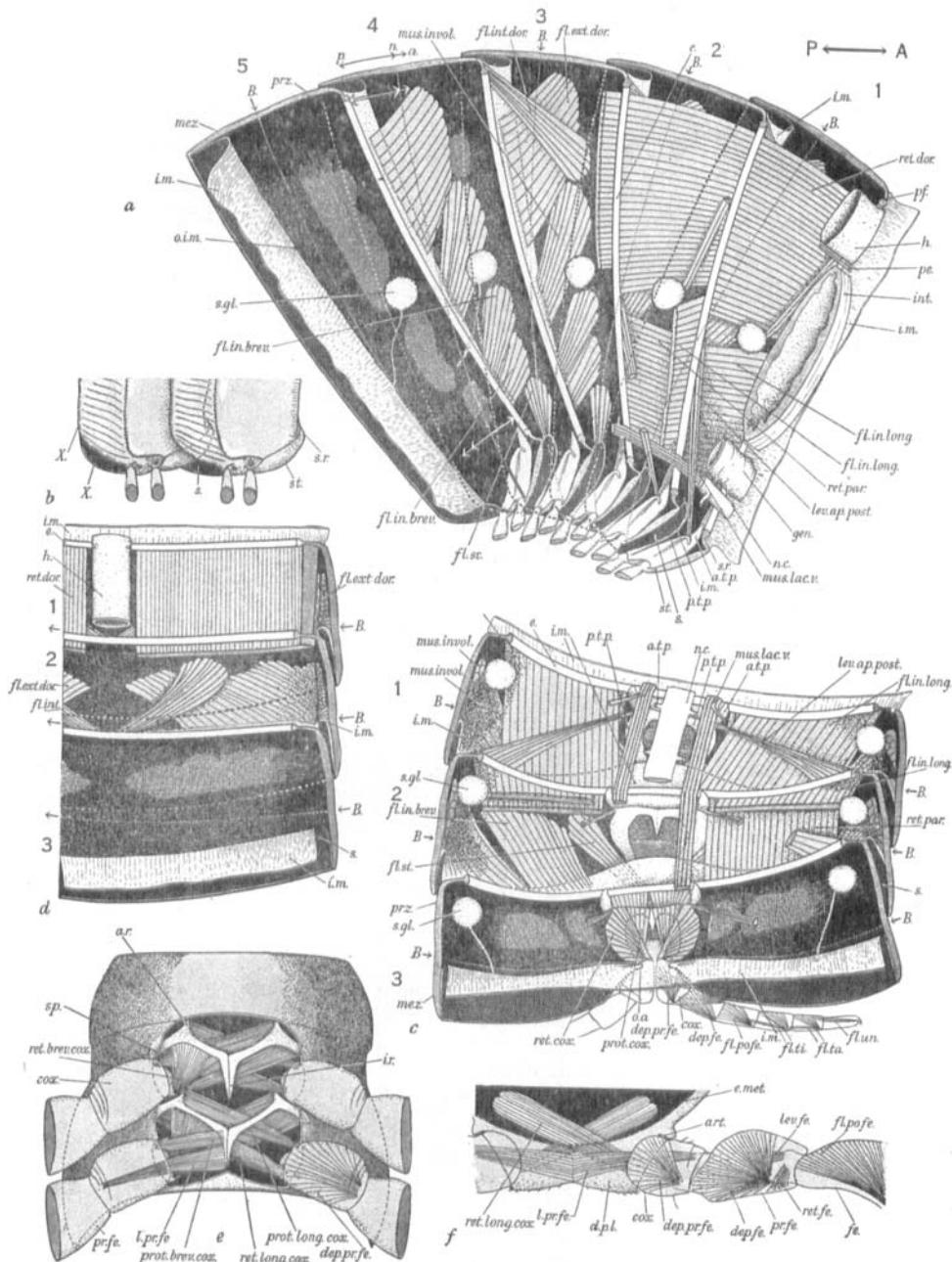
(d) Ventral view of the head end of *Poratophilus punctatus* (Juliformia) showing features permitting a close spiral.

(e-i) *Polydesmus angustus* (Polydesmoidea), (e) two diplo-segments of female, (f) anterior view of ring of male, full line showing position of leg when running, and dotted line the position when pushing or resting, (g) leg of male showing the muscles, (h) internal view of sagittal half of diplo-segment of female, legs foreshortened, (i) head end with head capsule on the collum 'c.h.' and the junction of collum and hypostoma.

(j-m) *Blaniulus guttulatus*, (j) two diplo-segments in lateral view; the body is straight, (k) rings 4-7 dorso-ventrally flexed, (l) three diplo-segments flexed towards the dorsal side as far as is possible, (m) three diplo-segments flexed in the lateral plane.

(n) *Ophistreptus guineensis* (Juliformia) showing maximum possible flexure in the lateral plane for comparison with fig. m.

(o-p) *Polymicrodon polydesmoides* (Nematophora), (o) ring of female in ventral view showing the movable sternites, (p) anterior view of diplo-segment of male showing position of leg when running.



TEXT-FIG. 3.

Figs. *a-d* show the skeleton and inter-ring musculature of a juliform millipede *Poratophilus punctatus*. The fat body, tracheae and malpighian tubes have been removed, and the heart, intestine, nerve cord and muscles are progressively cut back or removed, in the series of segments shown, which are taken from the middle of the trunk. White rulling indicates the site of muscle insertions on to the exoskeleton, white stippling shows the under surface of the overlapping part of the metazonite which is exposed to the exterior, black rulling shows cut surfaces of muscles, skeleton, etc., intersegmental membranes are lightly stippled and white in section and the tracheal pouches and inner edges of the prophragmae are white.

LEGEND TO TEXT—FIG. 3 (continued).

- (a) Internal view of a sagittal half of five rings when the body is flexed towards the ventral side.
 (b) Slightly oblique lateral view of the lower part of two rings to show the relationship of the sternites, the anterior end of the ring, and the groove B, when the body is held in a straight line.
 (c) Internal view of the ventral half of three rings bisected horizontally with the body flexed to the right.
 (d) Internal view of a dorsal sector of three rings bisected horizontally, the body being straight.
 (e) External view of ventral half of a ring of *Polydesmus angustus*, the tracheal pouches and extrinsic limb musculature exposed by removal of the ventral dilatations of the pedigerous lamina.
 (f) Posterior view of metazonite showing the insertion of the limb and the extrinsic and intrinsic limb musculature.

<i>a.</i>	most anterior position of dorsal edge of prophragma.	<i>mus.invol.</i>	musculus involvens.
<i>A.</i>	posterior free edge of metazonite.	<i>mus.lac.v.</i>	musculus lacuna ventrale.
<i>a.i.</i>	apophysis of involvens muscle.	<i>n.</i>	position of dorsal edge of prophragma or of dorsal edge of prozonite, when the body is straight.
<i>a.r.</i>	anterior ramus of tracheal pouch.	<i>n.c.</i>	nerve cord.
<i>a.t.p.</i>	anterior tracheal pouch.	<i>o.a.</i>	ring skeleton holding coxa.
<i>art.</i>	strong dorsal articulation of coxa and ring skeleton.	<i>o.i.m.</i>	origin of intersegmental membrane.
<i>B.</i>	constriction running round the ring.	<i>p.</i>	most posterior position of dorsal end of prophragma.
<i>C.</i>	mark running round ring parallel to prophragma.	<i>p.t.p.</i>	posterior tracheal pouch.
<i>c.h.</i>	concavity on column articulating with head capsule.	<i>pe.</i>	pericardial floor.
<i>col.</i>	column.	<i>pf.</i>	prophragma.
<i>cox.</i>	coxa.	<i>po.fe.</i>	postfemur.
<i>cox.s.</i>	coxal sac.	<i>pr.fe.</i>	prefemur.
<i>D.</i>	anterior end of prozonite.	<i>prot.brev.cox.</i>	protractor brevis coxae.
<i>d.i.</i>	dorsal insertion of involvens muscle from succeeding ring.	<i>prot.long.cox.</i>	protractor longus coxae.
<i>d.p.l.</i>	dilatation on pedigerous lamina opposite leg bases.	<i>prot.cox.</i>	protractor coxae.
<i>dep.fe.</i>	depressor femoris.	<i>prz.</i>	prozonite.
<i>dep.pr.fe.</i>	depressor prefemoris.	<i>r.</i>	level of ridge between sockets for head capsule and ring two.
<i>e.</i>	bare inner edge of prophragma.	<i>r.2.—r.7.</i>	second—seventh ring.
<i>e.met.</i>	edge of metazonite.	<i>ret.brev.cox.</i>	retractor brevis coxae.
<i>fe.</i>	femur.	<i>ret.cox.</i>	retractor coxae.
<i>fl.ext.dor.</i>	flexor externus dorsalis.	<i>ret.cox.s.</i>	retractor of coxal sac.
<i>fl.fe.</i>	flexor femoris.	<i>ret.dor.</i>	retractor dorsalis.
<i>fl.in.brev.</i>	flexor inferus brevis.	<i>ret.f.e</i>	retractor femoris.
<i>fl.in.long.</i>	flexor inferus longus.	<i>ret.long.cox.</i>	retractor longus coxae.
<i>fl.int. and</i>		<i>ret.part.</i>	retractor paratergalis.
<i>fl.int.dor.</i>	flexor internus dorsalis.	<i>ret.pr.fe.</i>	retractor prefemoris.
<i>fl.long.po.fe.</i>	flexor longus postfemoris.	<i>s.</i>	surface of overhanging posterior edge of tergite which is open to the exterior.
<i>fl.po.fe.</i>	flexor postfemoris.	<i>s.2., s.3.</i>	sternites of rings two and three.
<i>fl.st.</i>	flexor sternalis.	<i>s.g.</i>	stink gland.
<i>fl.ta.</i>	flexor tarsi.	<i>s.m.</i>	sternite of metazonite.
<i>fl.ti.</i>	flexor tibiae.	<i>s.pr.</i>	sternite of prozonite.
<i>fl.un.</i>	flexor unginculi.	<i>s.r.</i>	anterior upwardly directed sternal ridge on to which flexor sternalis pulls.
<i>gen.</i>	genital tube.	<i>sp.</i>	spiracle.
<i>h.</i>	heart.	<i>st.</i>	sternite.
<i>hy.(s.1).</i>	hypopharynx (sternite of ring 1).	<i>t.</i>	tubercle above articular facet of coxa.
<i>i.m.</i>	intersegmental membrane.	<i>ta.</i>	tarsus.
<i>i.r.</i>	internal ramus of tracheal pouch.	<i>th.</i>	thickened rim on edge of ring.
<i>int.</i>	intestine.	<i>ti.</i>	tibia.
<i>l.1(r.2).</i>	first leg (situated on ring two).	<i>tr.</i>	trochanter.
<i>l.2(r.3).</i>	second leg (situated on ring three).	<i>X.</i>	emarginated ventro-lateral edge of tergite.
<i>l.3(r.4).</i>	third leg (situated on ring four).	<i>Y.</i>	ventro-lateral part of constriction running round to the ring.
<i>l.4(r.5).</i>	fourth leg (situated on ring five).		
<i>l.5(r.5).</i>	fifth leg (situated on ring five).		
<i>l.pr.fe.</i>	levator prefemoris.		
<i>lev.ap.post.</i>	levator apophysis posticae.		
<i>lev.je.</i>	levator femoris.		
<i>mez.</i>	metazonite.		

rest of the ring (see also text-figs. 2*j* and *k*). The sternite is directed markedly upwards at the anterior end, particularly in the smaller species. The legs, arising on the posterior half of the fused sternites, lie level with the greater part of the 'ball', which is also the site of the insertions of the trunk muscles.

The endoskeleton consists of two pairs of tracheal pouches and the prophragma (white in text-fig. 3 and coarsely stippled in text-fig. 2). From the spiracles, situated lateral to the limb bases, the flattened tracheal pouches slope forward, reaching the anterior end of the sternite (text-fig. 3, *a.t.p.* and *p.t.p.*). The prophragma consists of an annulus projecting inwards from the anterior end of the prosomite, being formed by both sternal and tergal plates. It ends in a thickening, in section showing the form of a steel girder (*e* in text-figs. 2*a* and 3*a, c* and *d*). The sternal component of the prophragma forms an anteriorly and upwardly directed ridge *s.r.* from which the intersegmental membrane arises, and through this membrane the flexor sternalis muscles are inserted on to the sternum and pull on this ridge. The intersegmental membrane elsewhere arises near the external limit of the prophragma (text-fig. 3), so leaving both sides of the prophragma available for muscle insertions. Of the millipedes which have been examined, *Plusioporus sulcatus* possesses legs which are relatively longer and stronger than the rest (Table I, columns 4 and 8 and Pl. 53, figs. 24 and 25), and the legs of *Gymnostreptus tabulinus* are also strong. Their endoskeleton is correspondingly heavy; the prophragma of *G. tabulinus* (text-figs. 2*a* and *b*) is as wide and thick as it is in the larger *Poratophilus punctatus* with much shorter legs (text-figs. 3*a* and *c*); both species are drawn to the same scale.

It will be noted that the tapering curved form of the prozonite between C and D, and the position and shape of the prophragma, are admirably shaped to give rigidity and strength, greater than that provided by the rings of the other orders, with the possible exceptions of the Polydesmoidea (text-figs. 2 and 4) and Lysiopetaloidae. However, the differences between the inter-ring joints of the Juliformia and the Polydesmoidea and Nematophora, from the functional and structural aspects, are differences of degree rather than of kind, except for the presence of free sternites in the Nematophora.

Movements Between the Rings.

The action of the ball and socket joint outlined above is shown in text-fig. 3. The white arrows on ring 5 in text-fig. 3*a* of a dorso-ventrally flexed *Poratophilus punctatus* show the equal and opposite displacement on the dorsal and ventral sides, a similar displacement being seen in a horizontal bend in text-fig. 3*c*. The constriction B is slight, and at the degree of flexure shown the edges of the metazonites on the right almost reach the deepest part of the furrow B. The maximum lateral bending possible to *Ophistreptus* is shown in text-fig. 2*n*, where the edges of the metazonites have now slipped beyond the deepest part of the ill-defined furrow at B on the concave side of the bend. On the longer and less deep rings of *Blaniulus* the furrow is more marked and takes a postero-ventral sweep round the sides of the body (text-figs. 2*j-m*), thereby accommodating to a maximum the postero-ventral edge of the metazonite when the animal is flexed, as in text-fig. 2*k*. In the majority of Juliformia the furrow B does not take this backward sweep but remains parallel to the anterior edge of the prozonite. It is the ventro-lateral edge of the metazonite which is emarginated towards the furrow B (text-figs. 2*a* and *c*) and so in either case the downward bending of the body is facilitated. These features are functional necessities, without which a juliform millipede could not exert its characteristic powers. The two or three anterior rings of the body bearing only one pair of legs are similarly shaped and provided with a furrow B.

The different degrees of possible flexures in several directions are shown for *Blaniulus* in text-figs. 2*f-m*. An angle of 32° between the rings is shown at the

anterior end of the body in the nodding position (text-fig. 2 *k*) while a maximum turn through 36° is possible for most rings. A much smaller flexure can occur in the dorsal direction (text-fig. 2 *l*) because the greater length of the ring dorsally soon brings the edge of the metazonite into the furrow B, thus halting the bend. An intermediate degree of bending is possible in the lateral plane (compare the sizes of the tinted areas in text-figs. 2 *k*, *l* and *m*). A maximum horizontal flexure of 33° is shown in text-fig. 2 *m*, about 5½ rings being needed to complete a turn through 180°, but in millipedes with deeper, shorter rings the maximum flexure between rings is much less, about 13° for *Ophistreptus* (text-fig. 2 *n*), and 14 rings are needed here to complete a turn through 180°. However, owing to the shortness of the rings, a more acute bend of the body can be effected than in *Blaniulus*, as shown by text-figs. 2 *m* and *n*. Millipedes with short, deep rings are more flexible than those shaped like *Blaniulus*; the latter cannot negotiate pegs as close together, relatively, as those shown in text-fig. 1 *c*. The 'snake' millipedes do in fact twist and turn in a more conspicuous manner than do most Juliformia, but this is a matter of inclination and habit rather than of capacity.

Dorsso-ventral Bending.

When the body of a juliform millipede is straight, the legs of successive rings are well separated (text-fig. 3 *b* and Pl. 52, figs. 9 and 10), and each sternal plate can be seen to tip upwards into a deep cavity, limited by the inter-segmental membrane. On dorso-ventral flexure the sternite is pulled forwards and upwards. This movement is effected by the flexor sternalis muscles, which pull on the anteriorly directed ridge of the sternite through their insertion into the inter-segmental membrane (text-figs. 3 *a* and *c*, *fl.st.*), and by the flexor inferus longus, *fl.inf.long.*, both attached to the preceding ring, and by the levator apophysis posticae, *lev.ap.post.*, attached to the succeeding ring. Involvens, *mus.invol.*, and flexor inferus brevis, *fl.in.brev.*, contribute to this movement. Ventrally the rings are pulled together by the paired longitudinal *musculus lacuna ventrale*, *mus.lac.v.*, running the whole length of the body and attached to successive prophragma and tracheal pouch regions. The retractor paratergalis, *ret.par.*, doubtless assists this movement. The ventral surface of the body thus becomes folded in a zig-zag manner as shown in text-fig. 3 *a*, where each sternite (hatched) is folded against the inter-segmental membrane (white), and lies obliquely dorsal and posterior to the preceding sternite. The legs of successive rings thus become tightly packed together, limiting further flexure. The anteriorly directed slope of the flattened tracheal pouches (*a.t.p.* and *p.t.p.* in text-figs. 3 *a* and *c*) allows this folding to take place. It could not occur with horizontal sternites as are present in the Polydesmoidea.

The necessary rigidity between the rings of the Juliformia is amply provided for by muscles uniting successive prophragma dorsally and laterally (see the retractor dorsalis, *ret.dor.*, and retractor paratergalis, *ret.par.*, on text-fig. 3). The muscles in the ventral sector antagonize those in the dorsal sector, acting on opposite sides of the ball and socket joint. They also antagonize corresponding muscles in successive rings. The flexor muscles mentioned above and the rotational muscles mentioned below doubtless contribute to the rigidity.

The coxal joint of the leg bears a proximal head projecting into the ring, and the narrow neck below the head is gripped by the ring skeleton (text-fig. 3 *c*, *c.a.*) in such a manner that antero-posterior swinging of the coxa is freely possible, but the head cannot be withdrawn. Only two extrinsic muscles supply the leg, and they are inserted on to the corresponding tracheal pouch. The retractor coxae is attached to this head which acts as a lever working against the ring skeleton, a suitable provision in the cramped available space for extrinsic leg muscles (text-fig. 3 *c*, *ret.cox.* and *prot.cox.*). In the smaller Juliformia with average sized legs the segments of the legs are roughly cylindrical in shape, but in the large

Poratophilus sulcatus with short legs there is a compensatory deepening of the legs and their basal segments are flattened in the transverse plane. Were it not for this flattening, a tight spiral would be impossible, since the leg bases would occupy too much space.

Rotation between the Rings along the Long Axis of the Body.

Rotation of one ring upon the next is mediated primarily by a series of muscles extending obliquely from the middle part of the exoskeleton of one ring to the intersegmental membrane of the succeeding ring just short of its origin from the prophragma, the flexor externus dorsalis, *fl.ext.dor.*, involvens, *mus.invol.* and flexor inferus brevis, *fl.in.brev.*, their exoskeletal insertions being shown on ring 5 in text-fig. 3 *a* and on ring 3 in text-figs. 3 *c* and *d*. The flexor internus dorsalis, *fl.int.dor.*, antagonizes the larger flexor externus dorsalis, while involvens and flexor inferus brevis on the two sides of the body must clearly oppose each other. The insertion of these muscles into the intersegmental membrane allows them a little more space than would be available were they inserted directly on to the prophragma at the side of the retractor dorsalis muscles. The absence of flexores dorsalis internus and externus in the Oniscomorpha, where power of rotation between the rings on the long axis of the body is slight, suggests that these two muscles may be of particular significance for this well-developed movement in the Juliformia, and that involvens and flexor inferus brevis are concerned more with effecting dorso-ventral flexure. The exoskeleton is free of muscle insertions posterior to a line a little anterior to the waist B, see rings 3 and 5 on text-fig. 3. Only one part of the 'ball' at any moment lies anterior to this constriction (text-fig. 1 *a*) but muscles can only be inserted on the exoskeleton anterior to this level. The power of rotation of one ring upon the next depends largely upon the cylindrical form of the ball and socket, but is also dependent upon muscles holding the ball loosely in place (p. 305). The rings of a preparation devoid of muscles can be pushed together so tightly that they become wedged and no rotation is then possible. Such compression does not occur in life.

The inner rim of the prophragma is smooth and bare (text-fig. 3). Fat body surrounds the viscera and lies in sheets between and outside the muscle layers. When the body flexes, as in text-fig. 3 *a*, the ring volume in the ventral sector decreases while that of the dorsal sector increases. The viscera must therefore freely shift away from the concavity of any bend and slide along the bare ridges of endoskeleton.

The skeleton and muscles of the Spirostreptomorpha, illustrated here by *Gymnostreptus* and *Poratophilus*, do not differ in any major feature connected with locomotion from other members of the Juliformia. A small difference in the degree of separation of the parts of the paratergalis muscles in the Spirostreptomorpha and Juloidea has been noted by Silvestri (1903) and is referred to on p. 305, but a similarity of function remains.

SKELETO-MUSCULAR SYSTEM OF THE POLYDESMOIDEA.

Each ring of *Polydesmus* forms a complete and rigid unit, longer and less deep than in most Juliformia (Pls. 52, 53 and 55, and Table I, column 3), a condition associated with the presence of large keels and the need for unimpaired lateral bending (see below and p. 359). The simple form of the ball and socket inter-ring joint has been noted above. The anterior part of the sternal region is roughly horizontal (text-figs. 2 *e* and *h*) and does not tilt upwards anteriorly as in the Juliformia (text-figs. 2 *a*, *j* and *k*, and 3 *a*). Owing to the length of the ring, the 'ball' does not sink into the socket as far as the constriction B, and the internal rib of skeleton at the junction of pro- and metazonite does not participate in joint formation (text-figs. 2 *e* and *h*). The joint is strengthened by exoskeletal thickenings along the anterior and posterior margins of the ring (text-fig. 2 *h*).

Flexibility in *Polydesmus*, although conspicuous, is not as great as in the Juliformia. A lateral turn of about 25° between successive rings allows as acute a bend as is convenient to an animal possessing legs which project markedly sideways. The gaps which separate successive tergite keels are essential for lateral flexibility. Each keel slopes a little upwards towards the posterior end of the ring, and so the keels on the concave side of an acute lateral bend overlap each other in the manner of vertebrate zygapophyses and thus do not hinder the movement. Shorter rings could not carry such large keels.

The musculature of *Polydesmus* appears to be a simpler version of the same basic plan as seen in the Juliformia. The rings can be held together rigidly by the retractors dorsalis and paratergalis running between the anterior margins of the rings on the dorsal and ventro-lateral sides respectively. Lateral bending and rotation is mediated as before by flexores externus dorsalis and internus dorsalis, but these muscles are inserted on to the exoskeleton of the waist B. The shortness of the juliform ring necessitates a more anterior insertion for these muscles (see text-fig. 3 a). The retractors dorsalis and paratergalis must also contribute to lateral bending. Involvens and flexor inferus brevis shown in text-fig. 3 a, ring 4, which assist rotation of the juliform ring, are represented in *Polydesmus* by a single large involvens muscle inserted on to a localized apophysis (a.i. in text-figs. 2 e, f and i) on the anterior rim of the prozonite, which functionally replaces the widespread insertions of involvens and flexor inferus brevis of the juliform type. Dorsally the involvens fans out on to the upper posterior part of the keel (text-fig. 2 f, d.i.) of the preceding ring, the muscle thereby gaining a leverage which is impossible to the cylindrical juliform millipedes.

On dorso-ventral bending the flexor sternalis alone pull the sternite forwards and slightly upwards. There are no large flexor inferus longus muscles because each sternite is horizontal and cannot therefore be pulled forwards internal to that of the preceding ring. A close spiral is thus impossible (Pl. 55, fig. 42), and the degree of dorso-ventral bending is controlled by the length of each sternite (see p. 324); the movement is, however, facilitated by the absence of any mid-ventral overlap of the sternites when the body is straight, and by the length of the tergite being greater than that of the sternite (text-figs. 2 e and h). More acute bending by the anterior rings, achieved by a shortening of the sternites, results in a corresponding increase in the exposure of intersegmental membrane when the body is straight. A culmination of this tendency is seen in *Oniscodesmus* (text-fig. 4 f, and p. 321).

The Polydesmoidea push more powerfully than other millipedes (Table I, column 7, Table II, and pp. 326 and 340) and do so largely by their 'flat backs'. The form of the limbs, skeleton and muscular systems is correlated with this pushing power. The exoskeleton is very hard and inflexible. The dorsal surface is increased by the formation of keels, and the sculpturing (Pl. 55, figs. 38–41) must give rigidity to the integument. The under surface of each keel is convex in frontal section, a shape also conferring strength. The constriction B between pro- and metazonite is bare of muscle insertions except for the flexores externus dorsalis and internus dorsalis, and does not seem to be primarily an apophysis (text-fig. 2 h). Its major significance appears to be a strengthening rib which can transfer a thrust exerted by the legs to the strengthened dorsal surface. In the Juliformia, where the thrust is mainly exerted through the head end, there is no such strengthening rib, and the origin of the legs lies anterior to the constriction B and not ventral to it, for functional reasons which have already been noted (compare text-fig. 2 h with 2 a and c).

The poor powers of spiralling shown by *Polydesmus* allows the formation of stouter legs than is possible to the Juliformia with short rings and an ability to spiral tightly. The adult male *P. angustus* (text-fig. 2 f and Pl. 55, fig. 38) shows particularly stout legs compared with the Juliformia shown here on the plates and text-figures. In the pill millipedes (Oniscomorpha) the legs may be large, but they are markedly flattened in the transverse plane to allow curling up. The rigid pedigerous lamina of *Polydesmus* forms two transverse bulges lying across the posterior part of the sternal region (see text-figs. 2 f and h, and 3 e and f, d.p.l. and the middle rings on Pl. 53, fig. 22).

The limbs are inserted laterally on the ends of these dilatations, and not near the middle line as in other millipedes (compare text-fig. 2 *f* with 2 *b*, *d* and *p* and with text-figs. 3 and 4). The coxa is hinged to the ring so that it moves freely in the horizontal plane only, as in all millipedes. A strong projecting articulation between the coxa and the ring (text-fig. 3 *f*, *art.*) is situated below a dorsal tubercle lying just above the leg base (text-fig. 2 *e*, *t.*), and forms a strong point which, with the protractor and retractor longus muscles of the coxa (*ret.long.cox.* and *prot.long.cox.*, text-figs. 3 *e* and *f*), will resist a tendency for the distal end of the coxa to tip upwards when the animal is pushing with the dorsal surface. The joints between the coxa and prefemur and between the remaining more distal segments of the leg allow flexion and extension in a vertical plane but little horizontal movement.

The spiracles are directed laterally (text-fig. 2 *e*) and not ventrally as in most millipedes, and from them the tracheal pouches project inwards, forming a small anterior ramus, and a longer internal ramus which sweeps inwards, downwards and backwards as shown in text-figs. 2 *h* and 3 *e*. Tracheae arise only from the proximal section and anterior ramus, the rest forming a powerful ventral apophysis.

Four extrinsic muscles to each limb are housed in the dilatations on the sternal region *d.p.l.* The protractor longus coxae and retractor longus coxae, arising from the antero-ventral and postero-ventral edges of the coxa respectively, run diagonally upwards and forwards, dorsal to the inner rami of the tracheal pouches, to insert on the anterior ramus and proximal part of the tracheal pouch of the other side; the retractor is the larger (text-fig. 3 *e*, *prot.long.cox.* and *ret.long.cox.*). Two superficial muscles run out transversely from the inner ramus of the tracheal pouch, the levator prefemoris, *l.pr.fe.*, passing through the coxa to the dorsal edge of the prefemur, and the protractor brevis coxae, *prot.brev.cox.*, which inserts on the anterior margin of the coxa (text-figs. 2 *g* and 3 *e*). A powerful retractor brevis coxae arises postero-ventrally on the coxa and fans out over the tracheal pouch and internal ramus (*ret.brev.cox.*, text-fig. 3 *e*) situated between the superficial and the deep muscles. The depressor prefemoris from the ventral edge of the prefemur forms a wide fan over the ventral side and proximal edge of the coxa (text-fig. 3 *f*, *dep.pr.fe.*). The contrast between the four coxal muscles of *Polydesmus* and the two which are present in the Juliformia is shown by text-figs. 3 *c* and *e*. The intrinsic muscles (text-fig. 2 *g*) consist of a series of flexors all along the leg, but extensors also are situated in the basal segments (*l.pr.fe.* and *lev.fe.*). The depressor femoris and retractor femoris are inserted on to a powerful apophysis projecting well into the prefemur.

The lateral insertion of the limbs and spiracles enables the ventral surface of the body to be held closer to the ground than in other millipedes (compare text-fig. 2 *f* with 2 *p*, 4 *d-k* and Pls. 52 and 53, figs. 11, 22 and 25). In forcing a way into cracks which give way in one plane, both dorsal and ventral surfaces of the body may be in contact with the substratum, the legs and spiracles operating in the free lateral space. Over rough ground *Polydesmus* can stand up as shown in text-fig. 1, Part 2.

If the positions of the femur, postfemur, tibia, tarsus and claw shown by the dotted line in text-fig. 2 *f* are adopted, contraction of the depressor prefemoris and depressor femoris (text-figs. 2 *g* and 3 *f*), and partial relaxation of the distal flexors, must raise the body. Contraction of the levator femoris and less bulky but long levator prefemoris raises the leg during the forward stroke (Pl. 53, fig. 22). The powerful coxal muscles swing the leg forwards and backwards. The positions and crossing over of the longus muscles from the ventral edge of the coxa must also brace this segment against a force tending to elevate it which may be exerted by the distal parts of the limb when the animal is pushing. Thus the form of the legs, skeleton and muscles is well suited to exert a powerful downward and backward thrust by the legs, resulting when needed in an upward push against the substratum by the dorsal surface.

THE SKELETO-MUSCULAR SYSTEM OF THE ONISCOMORPHA.

Reference to text-fig. 1 *a* shows that when the body of a millipede is straight, the distances A-A, R-R and X-X from one ring to the next are all equal. When the rings flex the distance A¹-A increases, X¹-X decreases, while R-R remains unchanged. It has been shown above how elaborate are the ventral modifications of the Juliformia which make possible the reduction of the distance X¹-X, and it is clear from text-fig. 3 *a* that these modifications cannot be carried much, if any, further, and a closer contraction of the ventral surface is not possible along these lines. The Oniscomorpha have solved this problem of contracting the ventral surface in another way. The body of *Sphaerotherium dorsale* (text-fig. 4 *d*) and of *Glomeris marginata* represents little more than the upper sector of the rings shown in text-fig. 1 *a*, while the body of one of the largest species, *Sphaerotherium giganteum* from Zululand, 60 mm. long, does not exceed a semi-circle in transverse section (text-fig. 4 *e*). Flexure of the upper half rings in text-fig. 1 *a* can take place with no shortening of the ventral surface, which is now the distance R-R. The Oniscomorpha do in fact shorten the ventral surface when flexing, and they thereby attain a much tighter coil than is possible in the Juliformia.

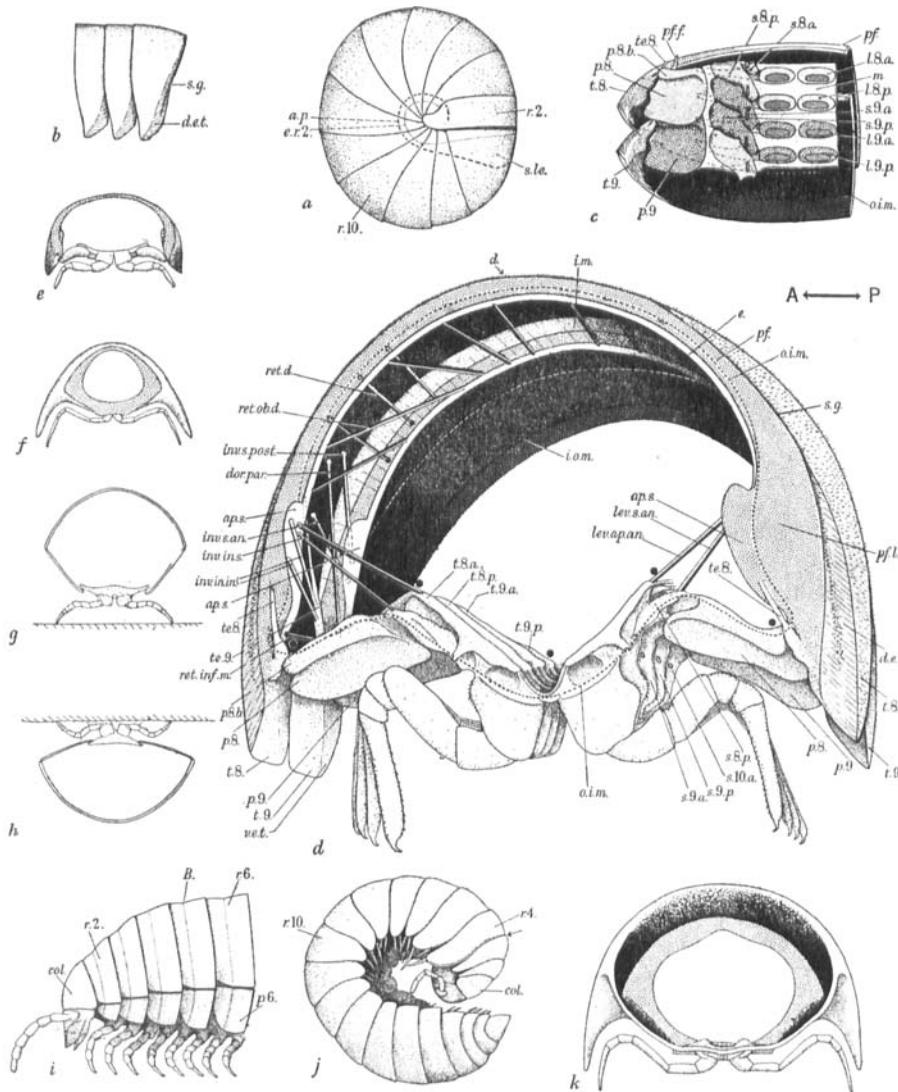
The suppression of most of the ventral half of the body cylinder has necessitated many modifications of the basic structures (p. 304). The 'ball' is no longer prevented from sinking deeper into the 'socket' by the shape of the preceding ring or by a waist B which would be inoperative. This waist is absent from the very rigid tergites. Lateral bending is limited, and powers of rotation of one ring upon another have been almost abandoned, because such movements cannot be combined with the development of structures needed for acute dorso-ventral flexure and the maintenance of rigidity by a half ball and socket joint.

The extent of the rigid prophragma is limited by the free pleurites and sternites. Dorsally the prophragma is well developed, much as in the Juliformia, and an upturned ridge along the anterior end of each pleurite represents the ventro-lateral sector of this structure (p.r.6 and the white unstippled ridges shown on the 7th, 8th and 9th pleurites in text-fig. 8 *e*). The absence of continuity between these two parts of the endoskeleton is compensated for by the presence of a large inward and forwardly directed flange, the apophysis squamosi lateralis (*ap.s.7*, *ap.s.* etc. on text-figs. 4 *d* and 8 *e*) from the lower lateral part of the prophragma, which carries muscles linking three or four successive rings.

The tergite is heavily constructed and resists deformation. The general form of the pleurite is a flat plate, but the details of its curves give the pleurite much greater rigidity than would be possessed by a thin flat plate which might easily be deformed by the upward pull of its muscles. Rigidity is also conferred upon the flat sternites by their minor curvatures, and by the anterior margins which in *Sphaerotherium* curl markedly upwards and backwards forming an apophysis (*s.e.*, text-fig. 8 *e*).

In the execution of dorso-ventral bending the ventral half of the prophragma is functionally replaced in part by a strong tendon, arising externally from a pillar on the edge of the tergite, and from the internal aspect sloping anteriorly from the flexible junction between pleurite and tergite (*te.6*, *te.7*, etc. on text figs. 4 *d* and 8 *e*). This tendon passes across the prophragma, lying just anterior and ventral to the lower border of the apophysis squamosi lateralis, and reaches the apophysis of the next anterior ring.

A shortening of the ventral surface is made possible by overlapping sclerites and by five longitudinal hinges marked by black dots in text-fig. 4 *d*. A pair of pleurites is horizontally hinged to the tergite. Two pairs of sternites, bearing spiracles and tracheal pouches, lie lateral to the leg bases, the outer margins of the sternites being covered by the pleurites. The parts are situated so that the under surface is folded like an inverted W in section. The leg bases, elongated transversely (Pl. 53, fig. 17), particularly in the larger species (text-fig. 8 *e*), are almost surrounded



TEXT-FIG. 4.

(a-d) *Sphaerotherium dorsale* (Oniscomorpha), (a) rolled up, in side view. The heavy dotted line indicates the position of the union between tergites and pleurites, and the lightly dotted line shows the margin of the shield (tergite 2) over which the lateral tergite wings of succeeding rings fit; (b) lateral view of three tergites when the body is straight to show their ventro-lateral attenuation and the part (hatched) covered in the flexed position; (c) diagram of the ventral aspect of two rings, the legs are cut off, the leg bases, sternites and tergite of one ring are heavily stippled; the parts shown correspond with those seen in fig. d, the preparation is slightly stretched to expose the whole of the sternites laterally, their lateral lobes in life tuck under the pleurites; (d) oblique anterior view of a slice of the skeleton of the middle region of the body comprising two tergites and the associated skeleton lying immediately below them, a plan of the parts in ventral view is shown in fig. c, the directions in which the inter-ring muscles pull are shown diagrammatically, the retractor obliquus dorsalis 'ret.ob.d.' is represented by a fan of five lines, and the retractor dorsalis externus 'ret.d.' by three parallel lines, on the animal's right; the white interrupted line shows the origin of the intersegmental membrane at the anterior end of the ring.

- (e) Anterior view of a ring of *Sphaerotherium giganteum* for comparison with fig. d.
 (f) *Oniscodesmus fuhrmanni* (Polydesmoidea) anterior view of diplo-segment.

by flexible pedigerous membrane (*m.* in text-figs. 4 *c* and 8 *e*). The staggered position of the parts of one ring are shown by heavy stippling in text-fig. 4 *c*. Successive pleurites overlap backwards, while the sternites do so in a forward direction. The rounded ridge on the anterior end of the pleurite, *p.8.b.* in text-figs. 4 *c* and *d*, slides against and dorsal to the preceding pleurite. When the body flexes dorso-ventrally the ventral elements are raised, so that they occupy the level R-R in text-fig. 1 *a*, all pleurites and sternites slide together more closely, overlapping in the manner described, and the flexible pedigerous membrane folds so that successive legs, which are markedly flattened in the transverse plane in the larger species, become tightly packed together, and lie back in the space *s.le.*, text-fig. 4 *a*, which is particularly large below the anal segment (see also Appendix).

The closeness of the dorso-ventral flexure achieved by *Glomeris* and *Sphaerotherium* is well known (text-fig. 4 *a* and Pl. 54, figs. 32 and 34). The ventro-lateral extensions of the tergites are emarginated anteriorly on the outer side (*d.e.t.* in text-figs. 4 *b* and *d* and see Pl. 54, figs. 29–33) and posteriorly on the inner side, *v.e.t.*, so that they fit together exactly, covering an anterior flange from the second ring (dotted line in text-fig. 4 *a*, and Pl. 54, figs. 29, 32 and 34) which butts against the lateral parts of the pleurites, the whole forming a very resistant ball. As noted by Langner (1937), a transverse groove lies just behind the anterior edge of each tergite, and a corresponding ridge on the inner side of the overlapping posterior margin. This groove in *Sphaerotherium dorsale* lies just behind an irregular row of coarse spines (*s.g.*, text-figs. 4 *b* and *d*). As the animal rolls up the free posterior overlap of the tergite slides forwards over the tergite behind it until the ridge snaps into the groove, so locking successive tergites and preventing them opening out too far.

LEGEND TO TEXT-FIG. 4 (continued).

(*g–i*) *Polyzonium germanicum* (Colobognatha), (*g*) and (*h*) show alternative positions of the skeletal elements and legs, in (*h*) the animal is holding on to the underside of a rock surface; (*i*) anterior end of the body in lateral view.

(*j–k*) *Glomeridesmus mexicanus* (Limacomorpha), (*j*) lateral view of dead specimen showing the manner of rolling up, the posterior parts can cover the head end as far as the arrow; (*k*) posterior view of diplo-segment. The prophragma is stippled in black, the inner side of the posterior edge of the metazonite situated beyond the origin of the intersegmental membrane is stippled in white on figs. *c* and *d*.

For key to lettering of muscles see legend to text-fig. 8, p. 355.

<i>a.p.</i>	level of articulation of pleurites and tergites.	<i>pf.l.</i>	lateral flat expansion of prophragma.
<i>ap.s.</i>	apophysis squamosi lateralis on prophragma.	<i>r.2, r.4, r.6,</i> <i>r.10.</i>	2nd, 4th, 6th and 10th ring of body.
<i>an.inv.s.</i>	pars antica musculus involventis superi.	<i>s.g.</i>	spines near anterior border of tergite behind which lies a groove.
<i>B.</i>	furrow across ring.	<i>s.le.</i>	enclosed space in which legs fold back.
<i>col.</i>	collum.		
<i>d.</i>	mid-dorsal line.		
<i>d.e.t.</i>	antero-dorsal emargination of lateral part of tergite.	<i>s.7.a.</i> <i>s.7.p.</i>	anterior sternite of 7th ring. posterior sternite of 7th ring.
<i>e.</i>	bare inner edge of prophragma.	<i>s.8.a.</i>	anterior sternite of 8th ring.
<i>e.r.2.</i>	edge of flange on ring 2 which fits under the lateral projections of the tergites.	<i>s.8.p.</i> <i>s.9.a.</i> <i>s.9.p.</i>	posterior sternite of 8th ring. anterior sternite of 9th ring. posterior sternite of 9th ring.
<i>i.m.</i>	intersegmental membrane.	<i>t.r.2, t.r.6.</i>	tergites of rings 2 and 6 respectively.
<i>m.</i>	flexible membrane between sclerites.	<i>t.8, t.9.</i>	tergites of 8th and 9th ring.
<i>o.i.m.</i>	origin of intersegmental membrane	<i>t.8.a.</i>	anterior tracheal pouch of 8th ring.
<i>p.6, p.8, p.9</i>	pleurite (paratergite) of 6th, 8th and 9th ring respectively.	<i>t.8.p.</i>	posterior tracheal pouch of 8th ring.
<i>p.8.b.</i>	boss of pleurite of 8th ring which slides over and against the preceding pleurite.	<i>t.9.a.</i> <i>t.9.p.</i>	anterior tracheal pouch of 9th ring. posterior tracheal pouch of 9th ring.
<i>pf.</i>	prophragma.	<i>te.8.</i>	tendon arising from tergite 8.
<i>pf.f.</i>	forwardly directed edge of apophysis squamosi lateralis.	<i>te.9.</i>	tendon arising from tergite 9.
		<i>v.e.t.</i>	postero-ventral emargination of tergite.

The half ball and socket joint between the rings of an oniscomorph cannot prevent the ball from sinking deeper into the socket in the same way as in the Juliformia. Instead the prophragma at the ventro-lateral angles is greatly expanded (*p.fl.*) and here the origin of the intersegmental membrane (*o.i.m.*, the black interrupted line in text-fig. 4 d) is displaced inwards. The musculature, described below, forms a fairly solid ventro-lateral mass, triangular in section, situated between the pleurites and lateral body wall. The flat expanse of prophragma pushes against this muscle mass preventing telescoping of the rings, and the origin of the intersegmental membrane so near to the apophysis squamosi lateralis results in the muscle mass being covered by this tough smooth membrane and thereby protected. The resistance afforded to telescoping is less effective than it is in the Juliformia. There are momentary changes in body length of 10 per cent in *Glomeris*, but the body can be well extended when walking fast or when progressing against a load.

End sternite and tracheal pouch are united around the spiracle, and together form a rigid whole. From the antero-lateral border of the base of the coxa an upward strut is horizontally hinged in the transverse plane to a projection from the tracheal pouch and sternite (text-fig. 8 f, hi.). The hinge allows the coxa to swing backwards and forwards, and the strut prevents the base of the leg from becoming displaced upwards into the body. When the leg is protracted, the antero-lateral angle of the coxa butts up against the lobe of the sternite which is directed towards the middle line (text-fig. 4 c).

Muscles in the Juliformia are inserted closely on to the surface of the endoskeleton, but in the Oniscomorpha they are attached to thick fascia covering the prophragma, its apophyses and the tracheal pouches, and the endoskeleton is not readily seen from the internal aspect. The muscles of *Glomeris* have been described by Silvestri (1903). Those of the larger *Sphaerotherium* are described here for the first time; the musculature of *S. giganteum* and *S. dorsale* appears to be essentially similar, although only the former species has been examined in detail. The muscles are shown in text-figs. 4 d and 8 e.

The *retractor dorsalis, ret.d.*, is much less massive than it is in the Juliformia. It is largely lateral in position in *Glomeris*, a few strands extending dorsally towards the heart, and in *Sphaerotherium* this muscle is wholly restricted to the lateral region, see section B on text-figs. 8 d and e. The shortness of the oniscomorph body may have reduced the power required from this muscle compared with longer bodied animals.

The very limited powers of rotation between the rings of an oniscomorph on the long axis of the body is correlated with the form of the inter-ring joint, and *flexores dorsalis* and *externus dorsalis* are absent.

A bulky *retractor obliquus dorsalis, ret.ob.d.*, is situated internal to the *retractor dorsalis*, inserting on the inner edges of successive prophragmata. Dorsally its muscle strands on either side of the heart run longitudinally between the rings, but laterally the strands fan out antero-ventrally, inserting on the prophragma as far down as the apophysis squamosi lateralis. This muscle must provide a considerable part of the force required to pull the tergites together ventrally, and is complementary in its action to the *involvens* complex. The position of the *retractor obliquus dorsalis* internal to the *retractor dorsalis* allows more space for its action than would be obtained in the external position occupied by the *flexores dorsales* of the Juliformia.

In the Juliformia the muscles pulling on the ventral half of the prophragma which cause dorso-ventral flexure are the *flexor inferus longus, involvens* and *flexor inferus brevis* (text-fig. 3). The absence of a rigid ventral half to the ring in the Oniscomorpha necessitates different insertions for some muscles and alterations in others, causing dorso-ventral bending. From the apophysis squamosi lateralis the elaborate *involvens* muscles pull the ventral parts of the tergites together. The *pars antica* and *pars postica involventis superi, inv.s.an.* and *inv.s.post.*, extend forwards and upwards from the outer face and inner edge of the apophysis to the

lateral part of the preceding tergite, and the *pars supra* and *pars infra involventis inferi, inv.in.s.* and *inv.in.in.*, arising on the tendon from the pleurite-tergite junction, extend forwards and upwards to the prophragma and to the ventral part of the inner face of the apophysis respectively, thus pulling three successive tergites and pleurites together.

The lower ends of the tergites in *Glomeris* and in *Sphaerotherium* are pulled together also by the *retractor inferus mesotergiti, ret.inf.m.*, running longitudinally between successive prophragmata ventral to the apophyses squamosi laterales.

The muscles which raise the ventral skeleton are much more elaborate in *Sphaerotherium* than in *Glomeris*. The dorso-paratergalis, *dor.par.*, of *Glomeris* runs almost perpendicularly from the tergite to the middle of the pleurite, arising between the insertions of the two parts of *involvens superus* on the tergite. The sternites and tracheal pouches are indirectly raised by this muscle.

In *Sphaerotherium* the pleurite, sternites and tracheal pouches are raised by five separate levator muscles. The *dorso-paratergalis, dor.par.*, is situated almost as in *Glomeris* but a little more obliquely. *Levatores apophyses anticae and posticae* and *levatores sternales anticae and posticae* are attached to the dorsal part of the inner face of the apophysis squamosi lateralis, and extend obliquely inwards and downwards, diverging from one another. *Levatores apophyses anticae and posticae* are inserted on the dorso-lateral ends of the lateral rami of the tracheal pouches of the same ring, *lev.ap.an.* and *lev.ap.post.*, superficial strands of each muscle spreading along the dorsal edges of the lateral rami of the tracheal pouches *lev.ap.an.s.* and *lev.ap.post.s.*

The strap-like *levatores sternales anticae and posticae*, situated just ventral and posterior to the *levatores apophyses anticae and posticae*, extend to the postero-lateral margins of the sternites just behind the tracheal pouches, but owing to the staggered position of the sternites, *levatores sternales anticae and posticae* from one tergite run to the posterior sternite of the same ring and to the anterior sternite of the following ring respectively.

The pulling together of the ventral elements in *Glomeris* is effected by the *retractor paratergalis, ret.par.*, running longitudinally between the upturned anterior rims of the pleurites, and by muscles between the tracheal pouches. In *Sphaerotherium* a similar retractor paratergalis muscle is the smaller and most external of three performing this function. From the anterior edge of the pleurite a bulky *flexor inferus longus externus, fl.in.long.ex.*, runs forwards and outwards through the preceding ring to insert on the lower inner border of the apophysis squamosi lateralis. A *flexor inferus longus internus, fl.in.long.in.*, from the same origin on the pleurite runs forwards and outwards through two rings to insert on the lower border of the next apophysis squamosi lateralis. The component strands of the *flexor inferus longus internus* are united by a tendon situated transversely through the muscle half-way along its length, tying its edge to the upturned rim of the pleurite which it crosses (tendon not shown in text-fig. 8 e). These two muscles are comparable with the *flexor inferus longus* of the Spirostreptomorpha, although differing in details (see p. 311).

The longitudinal pulling together of the tracheal pouches in *Glomeris* is effected by the broad *musculus apophysis sternalis externus* running between successive lateral rami, and by the narrow *musculus apophysis sternalis internus* between the small internal rami of the tracheal pouches. In *Sphaerotherium* the two rami of the tracheal pouches are about equal in size and lie in the transverse plane, *l.r.t.p.* and *i.r.t.p.*, in text-fig. 8 e, and the *musculi apophyses sternales internus and externus, a.s.in. and a.s.ex.*, are more equal in size, forming horizontal sheets uniting the dorsal margins of the tracheal pouches. Differential contractions of these muscles shift the tracheal pouches backwards and forwards (see below).

When the ventral surface of the body is raised, each pair of tracheal pouches is pulled together by the long and narrow pair of *sternalis intersecatus* muscles, *st.int.*, in both *Glomeris* and *Sphaerotherium*. These muscles run from the antero-dorsal

margin of each internal ramus of the tracheal pouch across to the opposite side of the body, inserting on the junction of the flexible pedigerous membrane and the anterior border of the coxa.

The locomotory movements of the Oniscomorpha include a backward and forward sliding of the coxae and tracheal pouches, the backward shift contributing a locomotory thrust (see p. 338). In *Sphaerotherium* an *obliquus medius*, *ob.m.*, extends obliquely forwards from the apophysis squamosi lateralis to the postero-ventral border of the lateral ramus of the posterior tracheal pouch of the preceding ring. A much shorter *obliquus anticus* arises from two zones on the anterior part of the pleurite and runs forwards and upwards to the corresponding position on the anterior tracheal pouch of the same ring. Contraction of these two muscles must pull the tracheal pouches backwards, besides stabilizing the free ventral elements.

In *Glomeris* the form and slope of the rami of the tracheal pouches differ from *Sphaerotherium* (see Silvestri, 1903, fig. 320). *Obliquus anticus* runs from the anterior margin of the pleurite to the anterior tracheal pouch of the preceding ring, and its contraction must pull this pouch backwards, as in *Sphaerotherium*. The alternate pouches however have no muscle giving a comparable pull. The *obliquus medius* runs backwards from the middle of the pleurite, and not from the apophysis squamosi lateralis, to the lateral ramus of the posterior tracheal pouch of the same ring, and must be concerned with the stability of the ventral parts in the absence of the set of four levator muscles possessed by *Sphaerotherium*.

The *protractor* and *retractor coxae* muscles run directly up from the anterior and posterior margins of the coxa to the corresponding internal ramus of the tracheal pouch (compare Silvestri, 1903, fig. 320 with text-fig. 8 e.). Since the coxa is inserted largely on to the flexible pedigerous membrane (see above) there is need for the coxa to be kept in alignment with the moving tracheal pouches. In *Sphaerotherium* the *obliqui sternales externus* and *internus* perform this function. *Obliquus sternalis externus*, *ob.st.ext.*, forms a sheet running between the antero-ventral border of the lateral ramus of the tracheal pouch and the anterior edge of the sternite (see the posterior sternite of ring 7, *s.7.p.*, in text-fig. 8 e.). It is balanced by *obliquus sternalis internus*, *ob.st.int.*, which forms a sheet between the postero-ventral border of the inner ramus of the tracheal pouch and the junction of the anterior border of the coxa with the pedigerous membrane. Contraction of the *retractor coxae* would tend to pull the coxa upwards were it not for the presence of the *obliquus sternalis internus*, which ensures that the *protractor coxae* fully protracts the leg. In *Glomeris* there is but one such muscle, the *obliquus sternalis anticus*. It must give comparable effects although it does not correspond exactly with either of the *obliqui sternales* of *Sphaerotherium*. The *obliquus sternalis anticus* of *Glomeris* runs backwards and inwards from the posterior part of the lateral ramus of each tracheal pouch to the junction of the pedigerous membrane and anterior border of the following coxa. In both *Glomeris* and *Sphaerotherium* a *retractor prefemoris* runs from the inner edge of the prefemur up to the internal rumus of the tracheal pouch (not shown in text-fig. 8 e.)

The skeleto-muscular system of the Oniscomorpha is remarkable in three respects. The free ventral elements and their muscles not only enable a tight dorso-ventral flexure to take place, but also allow the leg bases to be pulled backwards during the backstroke (p. 338). Additional muscles, besides the intrinsic and extrinsic leg muscles, are thereby made available for locomotory purposes. All the muscles running between the tracheal pouches, and from the tracheal pouches to other parts of the skeleton, must be concerned to different degrees in supplying this additional force.

Secondly the heavily constructed legs are inserted mainly on to flexible membrane, and are united with the skeleton by a single narrow strut, a most unusual condition for an arthropod with a heavy integument. The extrinsic leg muscles are spread over a wide coxal base, and if acute bending of the body is to be achieved, there is no space

available for rigid skeleton between the legs antero-posteriorly. The lateral shift of the sternites has made possible both stout leg bases and tight rolling up, and the elaborate series of muscles described above has made this type of limb insertion practicable.

The third striking feature is the linking together by the apophysis squamosi lateralis of a greater number of rings than is usual in millipedes. For example, the apophysis on the 9th ring of *Sphaerotherium* is united to the 8th tergite by the two parts of involvens superus, to the 8th posterior tracheal pouch by obliquus medius to the 9th anterior and posterior tracheal pouches by two levators, to the 8th posterior and 9th anterior sternites by two levators, to the 10th pleurite and tergite by the two parts of involvens inferus and to the 10th and 11th pleurite ridges by the two retractor inferus longus muscles (see also p. 328).

A convergent resemblance is shown between the Oniscodesmidae among the Polydesmoidea and the Oniscomorpha. *Oniscodesmus* is remarkably like *Sphaerotherium* in general features and can roll up fairly tightly (Silvestri, 1903, fig. 1). Each ring is short and shaped like a half-cylinder in section (text-fig. 4 f) with narrowing emarginated lateral wings as in the Oniscomorpha. On rolling up, the tips of these wings fit over a flange from the enlarged second ring as in *Sphaerotherium*. The inter-ring joints latero-ventrally form almost flat articulating facets instead of the deep ball and socket-like structures of other Polydesmoidea. The legs are less long than in *Polydesmus* and they fold back as in the Oniscomorpha into the space within the lateral wings (text-fig. 4 f). The ventral surface is rigid, as in other Polydesmoidea, unlike that of the Oniscomorpha. Rolling up is made possible by the sternal zone approaching the level R-R in text-fig. 1 a relative to the tergite, and by the rigid sternite being very short and separated from the next by a long intersegmental membrane. On dorso-ventral flexure the sternites pack together so that successive leg bases touch each other and the dorsal joints open out where the tergites overlap greatly, as in the Oniscomorpha.

In the Limacomorpha, which with the Oniscomorpha form the division Opisthania, the power of rolling into a ball is less perfect, although *Glomeridesmus*, with more segments than the Oniscomorpha, spirals fairly tightly (text-fig. 4 and Pl. 54, fig. 35). The form of the ring is superficially just as it is in the Oniscodesmidae, and in both the tergite portion of the rigid ring is 2·5 times the length of the sternite. The rings allow acute dorso-ventral bending but little lateral turning. A ring of *Oniscodesmus* (Polydesmoidea) is shown in text-fig. 4 f in anterior view for comparison with the posterior view of a ring of *Glomeridesmus* (Limapomorpha) in text-fig. 4 k. The convergent similarity between these groups is correlated with the solving of problems presented by rolling up in a similar manner. The ventral regions of *Oniscodesmus*, *Sphaerotherium* and a juliform millipede show three different methods of achieving marked dorso-ventral bending (see also p. 324).

THE SKELETO-MUSCULAR SYSTEM OF THE NEMATOPHORA.

The British *Polymicrodon polydesmoides* shows a remarkable convergent resemblance to *Polydesmus* (Pls. 53, 54, figs. 18 and 28), although possessing fundamental structural differences. *Craspedosoma rawlinsi* (Pls. 53, 55, figs. 20 and 45) has smaller keels and a slightly more juliform-like appearance, and keels are lacking in *Microchordeuma scutellare*. Their bodies are constructed so as to exert a powerful push largely by means of the 'flat back' as in the Polydesmoidea, and comparatively little force appears to be exerted in a juliform manner by the head end. Three pairs of spines on each ring are directed upwards and sideways in *Microchordeuma* and are carried out by the keels in other species. The relatively large spines of *Microchordeuma* are inserted on thickenings of exoskeleton, they can bend over at the bases, and the tips are very flexible; thus overlying litter cannot be impaled upon the spines. The anterior part of the body tapers more markedly than in the other orders so far considered (compare Pls. 52, 53, 55, figs. 9, 10, 18, 20, 22).

and 38) and the head, collum and marked 'neck' are less fitted to bear a powerful thrust than are the corresponding parts of the Juliformia. The tapering body enables the head end to be free when the thicker middle region of the body may be exerting a thrust on overlying dead leaves, as in the Polydesmoidea. The 27 leg-bearing rings are a little shorter and deeper than in the Polydesmoidea, and the overall shape of the body is a little longer (see p. 360).

The inter-ring ball and socket joint is as simple as in the Polydesmoidea, but owing to the ventral discontinuity of the sclerites and the tergal hoop being capable of slight deformation, the skeleton itself cannot entirely prevent one ring from telescoping into the next, and this contingency is controlled by muscles. However, the animals do not appear to use bulldozer-like tactics to the extent employed by the Juliformia, and therefore the need to resist a tendency to telescope cannot be so great.

Lateral bending occurs as in the Juliformia. The keels of *Polymicrodon* are smaller than in *Polydesmus* and butt close to each other on the concave side of a bend, the angle of flexure at each joint being less since the length of the ring is proportionately less (see the Juliformia, p. 310).

The Nematophora resemble the Juliformia in their power of spiralling tightly, but the provisions which allow of acute dorso-ventral bending differ from those existing in the groups so far considered. Each diplo-segment possesses two free median sternites, each of which carries a pair of legs posteriorly, as seen in text-fig. 2 o. When the body is straight the successive legs are equidistant from one another (Pls. 53, 55, figs. 20 and 45) and are not situated at alternate sized intervals as in the Juliformia (see text-fig. 3 b and Pl. 52, figs. 9 and 10). Ventrally the sternites are overlapped on either side by the tergite, and the sternites and their tracheal pouches slope upwards and forwards in a manner not unlike that of the rigid sternites and tracheal pouches of Juliformia (see text-fig. 3 a). The necessary reduction of the ventral surface on dorso-ventral bending (text-fig. 1 a) is accomplished by the sternites sliding over one another from before backwards : that is, in the opposite direction from that taken by the sternites of the Oniscomorpha. The movement continues until the posterior margin of one sternite impinges on the median papilla situated between and slightly anterior to the leg bases on the succeeding sternite (text-fig. 2 o and Pl. 55, fig. 45), so keeping the edge of each sternite from pressing directly upon the legs. Only a small exposure of the sternite remains, and the pairs of legs become tightly packed together. As in the Onisco-morpha the leg bases are moved posteriorly during the backstroke (p. 338), the sternites sliding over one another.

The skeletal features of the Polydesmoidea which resist dorso-ventral pressure (p. 313) are also present, but in a less marked degree, on the tergal part of the ring of many Nematophora Chordeumoidea.

Silvestri (1903) has described the muscles of *Callipus foetidissimus* which probably do not differ in essentials from those of *Polymicrodon* or *Craspedosoma*, which have not been investigated here. Since the sternites must be prevented from sinking upwards into the tergal hoop when the animal is exerting a push by the dorsal surface, a more elaborate complement of muscles would be expected to be present in the Nematophora than in the orders so far considered.

In *Callipus* the inter-ring muscles, retractor dorsalis and flexor inferus longus, are present as in the Juliformia (text-fig. 3 a), the presence of the latter being associated with the spiralling ability, in contrast to the Polydesmoidea, where this muscle is absent. The flexor externus dorsalis is present as in a juliform and the involvens is represented by the involvens medius. A juliform-like levator apophysis posticae is present, but in addition there is a levator apophysis anticae, both sternites being free. An elaborate additional series of involvens muscles is present, as in the Oniscomorpha, but differing from the latter in details, made necessary in both cases by the free ventral elements. In *Callipus* involvens inferus, involvens inferior

and involvens superus pass from the upper parts of one ring to the anterior tracheal pouch, the pedigerous lamina and anterior margin of the following ring respectively.

The tracheal pouches and sternites are pulled together, increasing their overlap, by the large musculus apophysis sternalis running from one tracheal pouch to the next. This muscle corresponds functionally with the musculi apophyses sternales externus and internus of the Oniscomorpha. The two dorso-sternal muscles of the Oniscomorpha, obliquus anticus and obliquus medius, are represented by six muscles extending in different directions from the apex and from the base of the tracheal pouches to several parts of the pleural region of the ring, in addition to the already mentioned levatores apophyses anticae and posticae. Musculus inferior lateralis anticus apophysis posticae, musculus inferior lateralis posticus apophysis posticae and musculus inferior apophysis sternalis anticae run almost vertically down to the edge of the paratergite (see Silvestri, 1903, figs. 319 and 324), so preventing the legs from pushing the sternites upwards.

The extrinsic limb muscles in principle resemble those of *Polydesmus* although differing in details, a similarity probably correlated with the ability to push by the dorsal surface. Four coxal muscles are present, the protractor longus coxae and retractor longus coxae crossing over to the opposite side, as in the Polydesmoidea. Length for these two muscles is made possible by the antero-dorsal elongation of the tracheal pouches and their apophyses, while length in the Polydesmoidea results from the more lateral insertion of the limbs. The protractor longus coxae of the Nematophora, arising from the external proximal angle of the coxa, extends to the apex of the apophysis of the tracheal pouch of the following sternite, a condition associated with the need for leverage and the shorter ring in the Nematophora. As in the Juliformia the insertion of the coxa into the ring is narrow and the coxa is provided with a lever-like flange.

SKELETO-MUSCULAR SYSTEM OF THE COLOBOGNATHA.

There is greater variation in external form in the Colobognatha, most of which are tropical, than in other orders of millipedes. *Dolistenus savii* is extremely long with about 87 rings, the keeled terga superficially resembling those of *Polydesmus* and *Polymicrodon*, while the British *Polyzonium* is shorter and 'fatter' than most juliform species.

The narrow head of *Polyzonium* is ventrally directed and the dorsal part of the collum is turned forwards, almost as in a juliform species when pushing (text-fig. 4*i* and Pl. 54, figs. 36 and 37). *Polyzonium* probably pushes mainly from the anterior end, and the collum, although small, forms a resistant cap at the front end, but owing to the marked anterior tapering of the body, the push is transferred to the dorsal side. Many of the functional principles governing the morphology of the several orders of millipedes considered above are employed together by *Polyzonium*. The tergites form fairly firm half cylinders, each hinged horizontally to a pair of pleurites, and two median sternites carrying the legs lie between each pair of pleurites. The sternites and pleurites are separated by flexible membranes. Each tergite tapers anteriorly, but forms neither a prophragma nor a rigid 'einschub-cylinder' as in the Juliformia, Polydesmoidea and Nematophora. In the dorsal photograph, Pl. 54, fig. 37, each tergite shows two high lights, between which lies the furrow B, which functions as in the Juliformia in resisting antero-posterior compression, but owing to the many flexible joints to each ring, the resistance in *Polyzonium* is less effective. The intersegmental membrane uniting one ring with the next is roughly cylindrical, while the hinge between the metazonite section of the tergite and pleurite (posterior to the furrow B in text-fig. 4*i*) forms on either side an outwardly directed projection, resembling in miniature the keels of the Polydesmoidea and Nematophora, although morphologically more ventral in position.

Each ring can alter its shape (text-figs. 4*g* and *h*). The more circular sectional form is shown by the skeleton devoid of muscles and by the animal when longitudinally

contracted or when twisting one ring upon another. The intersegmental membrane during such rotation can remain cylindrical in spite of the lateral angle in the metazonite, and the absence of a prophragma or other rigid internal flange shaped like the metazonite is doubtless correlated with the retention of marked powers of rotation of one ring upon another, in contrast to the Oniscomorpha.

The more flattened sectional form of the ring is shown by animals walking fast or spiralling tightly, or after the laying of a batch of eggs, but the most extreme flattening is shown by animals resting on rock surfaces in a chiton-like manner (p. 353). The curvature of a tergite can be altered giving a 10 per cent increase in body width. A raising of the ventral parts of the pleurites and of the sternites decreases the depth of the body, and gives the greatest cover for the legs. It has already been shown how an approximation of the body to a dorsal half cylinder, results in less intake of ventral surface being necessary in acute dorso-ventral bending. Thus the shape changes of *Polyzonium* combine the advantages of the cylindrical ring of the Juliformia with those of the rings approximating to a half cylinder in the Oniscomorpha and others, but this combination, achieved by freely moving joints, gives a lower overall rigidity to the body (see p. 303) and must limit the pushing powers. In the spiral position the sternites do little more than pack tightly together in contrast to their marked overlapping in the Nematophora and Oniscomorpha, and the spiral is less tight (Pl. 55, fig. 47).

The muscles of *Siphonothinus argentinus* have been outlined by Silvestri (1903) and those of *Polyzonium* probably do not differ greatly. A retractor dorsalis and a flexor inferus longus run between successive tergites and sternites respectively and are inserted on to their anterior margins. Movement between the rings and the raising of the ventral parts is mediated by involentes inferior, medius, superus and inferus running from the tergite to the pleurite, and to the pedigerous lamina of the following ring. The involvens complex mainly raises the ventral elements while in the Oniscomorpha it entirely serves the pulling together the ventral ends of the tergites. In the Nematophora the involvens muscles both raises the ventral elements and approximate the rings ventrally. A single pair of muscles moves the tracheal pouches and sternites of *Polyzonium* (see Verhoeff, 1928, fig. 728). The coxal insertion of the leg on the ring is wide, and there are only two extrinsic coxal muscles. (For leg structure and coxal sacs see p. 356 and text-fig. 8 c.)

STRUCTURES PERMITTING THE SPIRAL POSITION.

An ability to spiral tightly is most perfect in the Juliformia (Pl. 55, fig. 44) where the outer whorl can lie either outside or superimposed on the inner, giving a very compact form. This ability is least developed in many Polydesmoidea; *Polydesmus* spirals loosely at the anterior end only (Pl. 55, fig. 42). The nematophoran *Craspedosoma* spirals fairly tightly, as does *Lysiopetalum* (see Löhner, 1914, pl. 10, figs. 22 and 23), but the *Polydesmus*-like *Polymicrodon* spirals but loosely, and does so most readily at the anterior end, thus resembling *Polydesmus* or a partially curled *Lysiopetalum* (Löhner, 1914, pl. 10, fig. 24). *Polyzonium* spirals less tightly than the Juliformia and assumes its tightest position with reluctance (Pl. 55, fig. 47).

Verhoeff (1926) noted that rolling up in millipedes is accompanied by a ventral 'crumpling', and Attems (1926) pointed out the correlation between short sternites and a marked ability of dorso-ventral bending. It has been shown above how the ability to spiral is dependent upon four features enabling a ventral shortening of the body to take place. (1) Short sternites make possible the spiralling of the Oniscodesmidae (Polydesmoidea) and Limacomorpha, and the anterior rings of *Polydesmus* show shorter sternites than the posterior rings. (2) The Juliformia achieve a coil by means of their tilted sternites. (3) The Oniscomorpha, Nematophora and Colobognatha all use free sliding sternites. (4) The Oniscomorpha, Limacomorpha, and isolated examples among other groups tend to reduce their bodies to a dorsal half cylinder which facilitates bending.

In the Juliformia the nodding movement between the head, the first and the second segment takes precedence over movements in other planes which are slight. The levator and depressor muscles are massive while the flexor muscles are small (Silvestri, 1903). The four features referred to above which reduce the ventral surface in the several orders of millipedes are all seen at the anterior end of the Juliformia. The skeletal rings are interrupted ventrally on segments 1–3, forming hoops in the manner shown on text-fig. 2 *d*, each ending in pointed flanges which can overlap so as to leave only the ruled facets exposed in a manner reminiscent of oniscomorphan tergites (text-fig. 4 *b*). The fourth segment possesses a narrow ventral bridge. The sternite of segment 1 (collum) forms the hypostoma, *hy* (*s.1*), and the sternites of segments 2 and 3 are free, flat and tilted, forming plates no thicker than the legs they carry at their free ends. The sternites are united by long stretches of intersegmental membrane. The width of the body anteriorly is little narrower than it is in the middle (Pl. 53, figs. 23 and 24), the collum being slightly wider than the second segment, but the depth of the anterior rings is less than in the middle region of the body (Pl. 52, figs. 9, 10, 11 and 16) and much of the flexible intersegmental membrane (heavily stippled in text-fig. 2 *d*) lies near the level R–R in text-fig. 1 *a*, where least reduction of the ventral surface is required. The British Julioidea resemble the Spirostreptomorpha in these respects, and the Spiroboloidea, although showing the same type of modifications, differ in detail. Since a posterior position of the legs is necessary for the accommodation of the head in the spiral position, the possession of two free sternites anteriorly eliminates the presence of a long uninterrupted stretch of soft integument behind the head ventrally when the body is straight. The single free sternite of segment 2 of *Polydesmus* (text-fig. 2 *i*, *s.2*) serves the same purpose. The Oniscomorpha tuck the head well in on assuming the ‘pill’ position. Ring 2 (the shield) of *Sphaerotherium* lacks a rigid pleurite, the first three sternites extend forwards, one outside the next, at the sides of the head and the head itself is short.

There is as yet no agreement concerning the nature of the apparently single anterior segments of millipedes (see p. 349). If they are indeed modified diplo-segments which have undergone reduction in the number of their limbs, the requirements for tight coiling may have been correlated with such a reduction. Reference to text-fig. 2 *d* and Pl. 55, fig. 44 shows the small length occupied by the ventral surface of the anterior rings in the spiral position of the Juliformia. The head when tucked in extends back to a level just in front of the two pairs of legs on ring 5. If the number of legs on rings 2–4 was doubled, the ventral surface could not be longitudinally compressed anteriorly to the extent shown, the head and anterior legs could not pack into so small a space, and consequently the body coil could not be so tight. The head in the Colobognatha is smaller than it is in all other millipedes (compare Pls. 52, 53, 54, figs. 9, 22, 26, 31 and 36 and text-figs. 2 *d* and 4 *i*), it projects backwards less far in the flexed position, and in consequence there is room for two pairs of legs on ring 4 (as also suggested by Brölemann, 1935), in contrast to the Juliformia, Oniscomorpha and Nematophora. In the Polydesmoidea with longer rings the stoutness of the legs still leaves no room anteriorly for more limbs without loosening the coil. Verhoeff (1901 *c* and 1926) has maintained that a second pair of legs on ring 4 has become converted into parts of the genital opening, a view not shared by Attems or Brölemann. Functional reasons for the evolution of diplo-segments are considered on p. 348.

THE COLLUM AND KEELS AND THE ABILITY TO PUSH.

The head in all millipedes is inclined antero-ventrally from the first segment, the tergite of which forms the collum (Pls. 52–55). In the Juliformia the collum is much longer dorsally than any other ring, and curves round the head on either side, ending in a lateral point (Pls. 52 and 53), completing a little more than a dorsal semi-circle (text-fig. 2 *d*). A strong inner transverse ridge lies at the level *r* on either side of the

collum. A socket is thereby formed for the head capsule, and the skeletal diaphragm partly covering the posterior face of the head fits into collum as occipital condyles fit into an atlas. A flat articular facet on either side of tergite 2 fits against the posterior side of the ridge r forming a second occipital condyle-like joint. The lateral facets on the second tergite resemble, in general form but not in detail, those of the Oniscomorpha, where again the dorso-ventral movement is the most important. The facets are most clear cut in the larger species.

The form of the collum in the Juliformia is suited to their bulldozer-like habit of pushing head on into leaf mould. The head end of the body when pushing against a resistance is held as in Pl. 52, fig. 16, and fig. 26 shows almost the same position except for the antennae; the middle of the dorsal surface of the collum lies at right angles to the direction of motion, and on an axis passing through the middle of the major part of the body. Such a stance is the most suitable for the transmission of the thrust from the legs, and the overlap of both head and second tergite by the collum suitably protects the joints between these parts. The antennae lie back with their distal ends, used for tapping the ground when walking, well away from contacts and giving also some protection to the eyes. The head capsule gives cover for the anterior pairs of legs.

The collum in *Polyzonium* functions in principle as it does in the Juliformia, but it is much smaller, less strongly constructed and lacks the neatly shaped articulations. The body tapers markedly at the anterior end (Pls. 54, 55, figs. 37, 48 and 49). Such features are correlated with the minute size of the head.

In the Oniscomorpha the collum is small and its overlap of the head and succeeding ring is slight, forming a neatly butting-up joint. When the head is extended in walking (Pl. 54, figs. 29 and 31) the collum forms an oblique loosely fitting cap across the back of the 'neck', but when the head is retracted the collum and anterior surface of the head together form a flat plate at the anterior limit of the shield (fused second and third tergites) (see Pl. 54, fig. 33). Possibly the animal exerts a weak push by the head, but the eyes are here fully exposed. A more powerful push is given by the shield when it is turned so that its dorsal surface becomes anterior, the head and collum facing ventrally (Pl. 54, fig. 33). The shield then functionally represents the collum of the Juliformia in transmitting a forward thrust.

The anterior ends of the Nematophora and Polydesmoidea are far less suited for pushing than in the orders just mentioned. The cheeks of the head capsule, and not the collum, form the widest anterior part of the body (Pls. 54, 55, figs. 28 and 38). In the species considered here the collum is no longer than the succeeding tergites (Pls. 53, 55, figs. 18, 20, 22 and 38), its lateral extent is less, and it forms a cap over the back of the 'neck'. The collum could not take much of a forwardly directed thrust (compare text-fig. 2*i* of *Polydesmus* with the juliform in Pl. 52, fig. 16). In *Polydesmus* the flat dorsal part of the collum is in series with the succeeding tergite keels, and the small pleurite uniting the lateral wing of the collum with the hypostoma below supplies the dorso-ventral rigidity which is useful in pushing with the 'flat back'. Little lateral movement occurs between the head and collum, the posterior part of the head capsule fitting into a hollow on the lateral wing of the collum (*c.h.* in text-fig. 2*i*) and butting closely on to the antero-lateral part of the second ring. These facets are shown unnaturally far apart in the figure, where the head is pulled forwards to display them. The support for the head provided by the collum and second segment leaves the animal capable of pushing forwards to some extent as well as upwards, but no evidence has been obtained to show that *Polydesmus* does in fact push forwards much with the head.

The Nematophora are even less suited for head-on pushing. The lack of union between the collum and hypostoma leaves a narrower and more flexible 'neck', allowing greater movement both in front and behind the collum, although the nodding movement still predominates. Verhoff (1926) has suggested that the anterior dorsal process on the collum of the Nematophora facilitates freedom of movement

of the head. The lateral flexibility of the 'neck' is more conspicuous in *Craspedosoma rawlinsi* than in *Polymerodon polydesmoides*, and both have good eyes in contrast to the blind *Polydesmus*. The Nematophora are also the fleetest millipedes which have been studied here. It is possible that the presence of eyes, faster running, and a tendency towards a carnivorous diet (p. 361) makes a flexible neck desirable, but this being gained, the animals can no longer push effectively by the head end.

The Nematophora Chordeumoidea and the Polydesmoidea do not burrow by pushing the head end into soil and leaf mould as do the Juliformia. The legs project too far for such a habit to be possible. The basic speciality appears to be the ability to push a way through matter which splits open along one plane, as does the damp layered mass of semi-decayed leaves on a woodland floor, or the bark and wood of decaying logs. The push is applied mainly by the dorsal surface or 'flat back', the keels when present providing both protection for the legs and a surface of application for the force. The British Nematophora occur in similar habitats, and their leg lengths appear to be correlated with the size of the keels. *Microchordeuma* lacks keels and has shorter legs than *Craspedosoma*, and *Polymerodon* has both longer legs and larger keels than *Craspedosoma* (see Table I, column 4). Since longer legs increases the pushing power of millipedes (p. 341), the development of keels must facilitate the acquisition of power as well as providing an increase in the pushing surface.

The evolution of keels has occurred several times in millipedes. The keels of the Polydesmoidea and of those Nematophora which possess them are very similar, and the rings in both are constructed in a manner suitable for the transmission of a thrust from the legs to the dorsal surface (pp. 313 and 352). The keels occurring in some Colobognatha are exaggerations of the projecting junctions of the tergites and pleurites seen in *Polyzonium* (p. 323). They also extend the dorsal surface and give cover for the legs, but the more ventral position of these keels may be related more with chiton-like habits than with protecting the legs during pushing by the dorsal surface (p. 353).

SKELETAL AND MUSCULAR SYSTEMS.

Thus the skeleto-muscular systems of millipedes are based in the main upon a common plan, which is modified in detail in the several groups in relation to different needs. In all groups adequate structures exist which will (1) transmit a pushing force to the head end or to the dorsal surface; (2) resist deformation and telescoping of the body segments; (3) combine strength with considerable flexibility of the body; and (4) permit a close or less close dorso-ventral flexure of the body. The latter feature is developed to different degrees and by different means in the several groups. Convergent similarities exist between members of distantly related groups (p. 358).

The musculature of the Colobognatha is the simplest shown by the several orders, and there are no elaborate endoskeletal features. Apart from the involvens muscles, this simplicity is probably primitive (see also p. 357). In other orders endoskeletal ridges for muscle attachments are variously developed, and are most conspicuous in the Juliformia and Oniscomorpha, and most specialized in the latter group.

The basic plan of the trunk musculature of Diplopoda differs from that of most Annelida and Arthropoda in two respects. Apart from the slender *musculus lacuna ventrale* of the Juliformia and the *retractor inferus longus internus* of *Sphaerotherium*, muscles do not cross more than one joint. The form of the skeleton and the development of the prophragma has subdivided almost the whole of the longitudinal musculature, and modified the insertions of many muscles.

Secondly, extrinsic leg muscles need to have access either to a lateral body wall, or to ventrally situated apodemes of some kind for their insertions. Peripatus and many Crustacea show examples of the lateral body wall being used in this manner.

The mid-ventral origin of the legs in millipedes and the shape of their rings render exoskeleton unsuitable for the limb-muscle insertions ; the lateral body wall is inconvenient to reach, and the latero-ventral region, were it used extensively, would necessitate the muscles pulling almost at right angles to the base of the limb. The insertions of the limb muscles on to the tracheal pouches allow these muscles to pull at advantageous angles from the leg bases. The development of endoskeleton in the form of tracheal pouches is thus as important for the limbs as for the tracheae, and may be correlated with the need for approximately mid-ventral limb insertions, which result in a minimum lateral projection of the legs (see also pp. 342 and 358).

The effect of size on the skeleto-muscular systems of millipedes is well shown by the differences between the Juloidea and the larger Spirostreptomorpha and by those between *Glomeris marginata* and *Sphaerotherium giganteum*. Skeletal facets and apodemes are more pronounced in the larger animals ; and legs may be wider and flatter, so accommodating muscles with relatively greater sectional areas which will provide adequate power for the heavier millipedes.

The muscles of *Sphaerotherium* are not only larger representations of those present in *Glomeris*, but there are more of them. Five levator muscles take the place of the dorso-paratergalis of *Glomeris*, and three muscles correspond with the retractor paratergalis of *Glomeris*. That these differences are related to size rather than to phylogeny is suggested by the presence of an undivided retractor paratergalis in both *Glomeris* and the Juloidea, and the parallel occurrence of additional flexor inferus longus muscles, differing slightly in details, in the Spirostreptomorpha and in *Sphaerotherium* (see text-figs. 3 a and 8 e). Since the weight of an animal is proportional to its volume, and the force put out by a muscle is proportional to its sectional area, the larger millipedes may be expected to possess more complex musculature than the smaller. Further effects of size are considered on pp. 343, 346 and 364.

THE MANNER OF DISCHARGE OF THE STINK GLANDS.

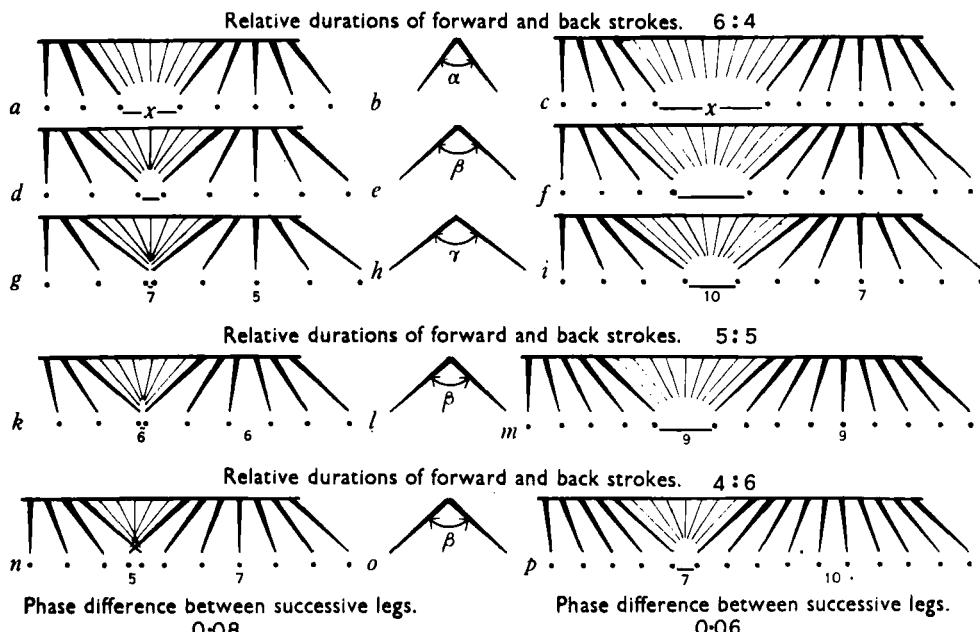
There is little information concerning the manner of ejection of fluid from the stink glands. Very rapid ejection, either as droplets or as a jet, is possible to the larger Juliformia and Lysiopetaloida (pp. 345 and 361). Silvestri (1903) shows small muscles passing to the outer section of the duct in some species, but no other muscles have been described. The reservoirs and ducts of the stink glands, which are lined with chitin, are shown in text-fig. 3 for the juliform *Poratophilus*. Each balloon-like reservoir lies in a space surrounded almost entirely by inter-ring muscles, and covered internally by the sheet of fat body separating the muscles and intestine. A sudden contraction of all these muscles would pull the rings together very tightly, so that at the inter-ring joints the 'balls' become less loosely placed in the 'sockets', and the pressure of these muscles on the reservoir must cause the expulsion of the contents. A similar principle is employed by snakes in expelling venom from their poison glands which lack muscles of their own. A more powerful ejection is to be expected from such a manner of discharge than would be caused by small muscles situated on the reservoir itself.

GENERAL CHARACTER OF THE GAITS.

Bethe (1931) noted that the backstroke of *Pachyiulus* was of much longer duration than the forward stroke, a relationship also shown by Lankester's (1904) drawings of *Archistreptus*. In Part 2, text-fig. 5 a 'bottom gear' gait of *Spirostreptus*, with a backstroke of relatively long duration, is contrasted with a gait of the chilopod *Cryptops* showing a backstroke of relatively short duration. Both are derivable respectively from the 'bottom' and 'middle gear' gaits of *Peripatus* (Part 2, text-fig. 4), the chilopod having also adopted a better method of stepping (Part 2, p. 102).

The Juliformia are capable of a very wide range of gaits (see p. 302 and entry for *Spirostreptus* in Part 2, Table 2, p. 105) and some species can be fairly fleet, but speed appears to be of secondary significance to power because the morphology of millipedes is mainly associated with the execution of powerful 'bottom gear' gaits (p. 352) and not with the faster ones. Except for some Nematophora, few millipedes need fleetness for securing food.

The duration of the backstroke relative to that of the forward stroke can be reduced in some instances to a figure which is smaller than that found in any arthropodan group, other than the Scolopendromorpha; Pl. 52, fig. 15 shows gait (7·6 : 3·3), the fastest which has been recorded, the figures within the brackets indicating the relative durations of the forward and backward strokes. However,



TEXT-FIG. 5.

Figures showing the effects of alterations in (1) the phase difference between successive legs (number of legs to a wave), (2) the relative durations of the forward and backward strokes, and (3) the angle of swing of the legs, on the type of gait employed by the Diplopoda. Propulsive legs are shown in black, recovering legs by thin lines.

it is the ability to employ powerful gaits with backstrokes of relatively long duration that is of particular significance to the Diplopoda, gaits in which the relative duration of forward and backstrokes readily reach (1·5 : 8·5). This necessitates very many legs to each metachronal wave (see below and Part 2, text-fig. 5, p. 107 for *Spirostreptus*, where many legs are pushing simultaneously against the ground, heavy lines, and few legs are in the recovery stroke, thin lines).

Text-fig. 5, Part 2 also shows that in both *Spirostreptus* and *Polydesmus* the positions of the propulsive limb tips on the ground are approximately evenly spaced, as they are in the Chilopoda (Part 3, text-figs. 1 and 5, pp. 122 and 129), and the distance between the footfall of the last propulsive leg of one metachronal wave and the first of the following wave (marked X in text-fig. 5) is little, if any, greater than the distance between any other two successive propulsive legs. This feature is seen in Pl. 52, figs. 9 and 11, where the distance X is marked by horizontal lines.

In other photographs shown the distance X is variable or a little longer than that between successive footfalls within one wave. Such a disposition of the points of support of the body has obvious advantages. If the distance X is large (text-fig. 5 c) the body will be less evenly supported; if X is too small the legs in the recovery phase will be crowded and mechanical interference may occur (text-figs. 5 g, k and n, and see Part 3, p. 138, where it is shown for *Scutigera* that this distance must not be too small). The evenness in spacing of occupied footfalls is not rigidly maintained by all arthropods in all gaits. It is lacking, for example, in *Peripatopsis* in Part 1, Pl. 15, fig. 12*, and the footfalls of *Lithobius* shown on Pl. 34, Part 3 lack the regularity of the diagram on text-fig. 1, Part 3. The Diplopoda also fail to maintain this even spacing with regularity, but the tendency to do so is nevertheless of importance.

The general effects of alterations in the relative duration of the backstroke, in the phase difference between successive legs and in the angle of swing of the leg on diplopod gaits is shown in text-fig. 5. On the left a phase difference between successive legs of 0·08 gives 12 legs to each wave, while on the right a phase difference of about 0·06 gives approximately 17–18 legs to each wave. The effects of three alternative angles of swing of the legs are shown above, and below the same angle is employed as in figs. d–f. Figs. a, d and g show how an increase in the angle of swing of the leg in gait (6·0 : 4·0) at a phase difference between successive legs of 0·08 decreases the length of X; fig. g is impracticable because X is too small and the optimum gait must be either as in fig. a or intermediate between figs. a and d, X becoming a little shorter than in fig. a. At a phase difference between successive legs of 0·06, however (right side of text-fig. 5), a similar increase in the angle of swing of the leg reduces X, but from a long distance in fig. c to an optimum one in fig. i.

The lower diagrams show the effect of increasing the relative duration of the backstroke from gait (6·0 : 4·0) to (4·0 : 6·0) at the same angle of swing as in figs. d–f, that is, employing a more powerful 'lower gear' (see Part 1, pp. 534 and 553), in which a greater number of legs push simultaneously. Comparison of figs. d, k and n and of figs. f, m and p shows a decrease in the length of X, but the gaits on the right are practicable, because X is never too short, while those in figs. k and n are not because X becomes either too short or non-existent. The propulsive legs cross over in fig. n, which is usually an impossibility to an arthropod, as noted in Part 2, p. 111 and Part 3, pp. 124 and 138.

The optimum length of the distance X is determined by two factors: (a) the distance between successive footfalls (which are very different in text-figs. 5 d and p) and (b) the number and length of the legs in each group performing the forward swing (there are 7–5 on the left and 10–7 on the right of text-fig. 5); a larger number may need a greater distance X if mechanical interference is to be avoided, unless the legs are very short.

It is clear that if X is to remain optimum, the employment of a fast gait with a backstroke of relatively short duration, such as gait (6·0 : 4·0), is best executed by a short metachronal wave, as in text-fig. 5 d, showing 7 recovering and 5 pushing legs, and a more powerful gait with a backstroke of relatively longer duration, such as (4·0 : 6·0), is best executed by a longer metachronal wave as in text-fig. 5 p where there are 7 recovering and 10 pushing legs. Similarly, further increases in the relative duration of the backstroke giving more powerful gaits (see Part 1, pp. 534 and 553) must be associated with further decreases in the phase difference between successive legs. No many-legged arthropod has been found to employ a phase difference between successive legs so small that only a part of a metachronal wave is accommodated along the body at one moment. Therefore an animal cannot be expected to employ very powerful gaits unless it possesses a large number of legs.

* The black spots on this figure mark limbs near or at the end of the backstroke, not all limbs touching the ground as in Parts 2, 3 and 4.

The optimum phase difference between successive legs for any one gait is necessarily related not only to the gait but also to the length of each ring and to the length of the legs. Short body segments and long legs will require many legs to each wave, or the distance X will be too small. If the execution of the same gait be compared in a series of Juliform millipedes, those in which the ratio of ring length to leg length is greatest show the shortest metachronal waves. In *Plusioporoides sulcatus*, *Ophistreptus guineensis* and *Blaniulus guttulatus* this ratio is roughly 0·3, 0·5 and 0·9, and when performing gait (5·8 : 4·2) the number of rings per wave is respectively about 8·5, 6·0 and 4·5 (see Pls. 52, 53, figs. 11, 25 and 27 where the pattern of the gaits (5·8 : 4·2), (6·1 : 3·9) and (5·0 : 5·0) does not differ greatly). Thus phase differences between successive legs of about 0·06–0·11 for the execution of the same gait in different juliform species are related to the body proportions. Further effects of the shape of segments are considered on p. 345.

The factors determining the phase difference between legs of a pair have been considered in Part 2, p. 110. In all gaits showing a backstroke of longer duration than the forward stroke the legs of a pair will be expected to move in phase with each other. This relationship has been found in all adult Diplopoda which have been examined. That it occurs even in the faster gaits with backstrokes of relatively shorter duration than the forward strokes (Pls. 52, 53, figs. 9, 10, 11, 15 and 25–26) probably indicates that these gaits are of lesser significance to the animals, and that the predominant use of 'bottom gear' gaits, together with the associated morphological specializations, has led to a loss of a primitive versatility in this respect such as shown by *Peripatus* (Part 1).

VARIATIONS IN THE LOCOMOTORY MOVEMENTS.

When a millipede is walking freely or harnessed to a sledge, the several metachronal waves of limb movements passing along the body are similar in general character although variable in details (see Pls. 52–55), and sometimes there is irregularity at the anterior and posterior ends of the body where the waves of limb movement tend to be shorter, as noticed by Bethe & Thorner (1933). The first few limbs may not be used, and when seeking escape the head and first few segments may be raised off the ground as in Pls. 52, 53, figs. 11 and 27. If an animal is saddled with weights giving uneven distribution of pressure, longer waves with longer relative durations of the backstroke may occur below the heavier part of the load, as in Pl. 52, fig. 13, where the longest waves with 16 propulsive legs lie below the heaviest part of the load. Reduction in the phase difference between successive legs (increasing the length of the wave) will not directly affect the speed (Part 1, p. 536), but wide differences in the actual duration of the backstroke in different waves at the same moment are an impossibility, although small differences can be compensated for by minor alterations as in other arthropods.

THE PATTERN OF THE GAITS AND THE PHASE DIFFERENCES BETWEEN SUCCESSIVE LEGS.

Millipedes tend to show their fastest gaits when walking freely in bright light, that is, when they are trying to escape as quickly as possible (see left side of column 6 in Table I). Under these conditions the Juliformia usually show gaits near (6·0 : 4·0) (see *Schizophyllum sabulosum* gait (5·7 : 4·3), *Ophistreptus guineensis* gait (5·8 : 4·2), *Cylindroiulus londinensis* gait (5·2 : 4·8) and *Plusioporoides sulcatus* gait (6·1 : 3·9) in Pls. 52, 53, figs. 9, 10, 11 and 25) but occasionally one as fast as (6·7 : 3·3) is displayed (fig. 15). The faster gaits of the Polydesmoidea and Nematophora lie between (5·5 : 4·5) and (6·5 : 3·5), Pls. 53, 55, figs. 18, 20, 22, 38 and 39. Löhner's photographs of *Lysiopetalum* (1914) show gaits (5·0 : 5·0) and about (6·7 : 3·3) for slow and fast running, but he did not interpret his pictures. The faster gaits of *Glomeris* and of *Polyzonium* are (5·7 : 4·3) and (6·4 : 3·6) respectively (Pls. 54, 55, figs. 29 and 48).

1	2	3	4			
Animal	Volume of ring or of 2 segments in cu. mm.	Length in mm.	Weight in gm.	Number of legs or leg-bearing rings	Depth of ring or of 2 segments	$\frac{\text{Leg length}}{\sqrt{\text{Ring volume or leg length}}}$
ONISCOMORPHA						
<i>Glomeris marginata</i> ..	22 6.5	14 10.5	0.15 0.09	9 rings 9 rings	3.4 3.4	1.1 1.1
JULIFORMIA						
<i>Ophistreptus guineensis</i> ..	500	175	26	60 rings	5.1	0.98
<i>O. guineensis</i>	355	155	20	—	5.1	—
<i>Plusioporus sulcatus</i> ..	195	138	11.7	55 rings	3.6	1.7
<i>Poratophilus punctatus</i> ..	190	90	9	44 rings	5.0	0.67
<i>Graphidostreptus judaicus</i>	75	135	(approx.)	76 rings	3.5	1.1
<i>Gymnostreptus tabulinus</i>	12.5	76	6.4 2.8	56 rings	4.4	1.3
<i>Cylindroiulus londinensis</i>						
var. <i>caeruleocinctus</i> ..	6.2	38	0.34	48 rings	3.4	1.1
<i>Tachypodioiulus niger</i> ..	5.3	38	0.25	43 rings	2.9	1.6
<i>Cylindroiulus londinensis</i>						
var. <i>caeruleocinctus</i> ..	1.5	20	0.08	38 rings	3.4	1.1
<i>Micropodoiulus scandinavicus</i> ..	1.4	22	0.05	43 rings	3.3	1.3
<i>Cylindroiulus punctatus</i> ..	0.54	19	0.035	45 rings	3.5	1.0
<i>Blaniulus guttulatus</i> ..	0.17	28	0.007	48 rings	1.6	1.02
NEMATOPHORA						
<i>Polymicrodon polydesmoides</i> ..	0.7♂ 1.2♀	15 17.5	0.02 0.027	27 rings	1.9♂ 2.2♀	2.5♂ 1.7♀
<i>Craspedosoma rawlinsi</i> ..	0.97♀	18	0.025	27 rings	1.8	1.5
<i>Microchordeuma scutellare</i>	0.12♀	8.5	0.005	27 rings	2.0	1.37
POLYDESMOIDEA						
<i>Polydesmus angustus</i> ..	2.2♂ 2.7♀	20 —	0.08 0.08	17 rings	1.3♂ 1.4♀	2.3♂ 1.7♀
<i>P. angustus</i> (young) ..	1.4	15	0.035	17 rings	—	1.5
<i>P. angustus</i> (young) ..	0.83♀	13	0.022	17 rings	—	1.5
<i>P. angustus</i> (young) ..	0.42♂	10	0.008	17 rings	—	—
<i>Polydesmus coriaceus</i> ..	0.47	13	0.015	17 rings	1.1	1.6
COLOBOGNATHA						
<i>Polyzonium germanicum</i>	0.65	11	0.012	36 rings	3.7	0.69
COLEOPTERA						
<i>Cabarus violaceus</i> ..	—	26	0.55	3 pairs	1.0	—
<i>Helops laevioctostriatus</i> ..	—	10	0.07	3 pairs	0.9	—
CHILOPODA						
<i>Stigmatogaster subterranea</i>	2.1	70	0.07	79 pairs	1.0	0.75
<i>Cryptops anomalans</i> ..	22	46	0.98	21 pairs	0.5	1.3
<i>Lithobius forficatus</i> ..	11	24	0.72	15 pairs	0.7	2.0
ONYCHOPHORA						
<i>Peripatus novaezealandiae</i>	20	42	0.26	15 pairs	0.6-2.0	0.5
VERTEBRATA						
<i>Lacerta viridis</i>	—	—	14.5	—	—	—
Domestic mouse ..	—	—	26	—	—	—
Golden hamster ..	—	—	99	—	—	—
Domestic cat	—	—	5450	—	—	—

TABLE I.

Data relating primarily to representatives of the several orders of Diplopoda, but with entries concerning ring volume. The figures in columns 1, 3 and 4 are based upon the middle rings of the body (different specimens are not equal, their mean has been taken for the calculation; the entry for *Stigmatogaster* refers to a living, to the longitudinally contracted state. The figures in columns 5 and 6 represent the range which has been most usually exhibited. The figures in columns 7, 8 and 9 refer to single performances of the given specimens which are slightly different but of the same order, and the examples given show comparisons between species.

Number of pairs of legs per metachronal wave		Range of gaits	Pulling force Body weight $\left(\frac{f}{w}\right)$	One ring		Maximum force in gm. exerted by legs per mm. ² T.S. area of body	Pulling force in gm. exerted by body per mm. ² T.S. area of body
Fast gaits unladen	Slow gaits max. load			Pulling force exerted in gm.	Body weight carried in gm.		
6-7	9	5·7 : 4·3 -(1- : 9+)	12	0·20	0·016	0·12	—
6-7	9	5·7 : 4·3 -(1- : 9+)	13·3	0·13	0·010	0·19	—
12	25	6·7 : 3·3 -2·9 : 7·1	2·4	1·06	0·44	0·37	—
—	—	—	2·7	—	—	0·40	—
16	52	6·1 : 3·9 -1·5 : 8·5	7·2	1·53	0·21	1·2	—
—	—	—	—	—	—	—	—
14	42	5·7 : 4·3 -1·7 : 8·3	6·8	0·57	0·084	1·5	—
—	—	—	—	—	—	—	—
13	28	6·3 : 3·7 -2·6 : 7·4	14·7	0·109	0·0074	0·66	—
16	28	6·2 : 3·8 -2·8 : 7·2	20·5	0·119	0·0058	0·82	—
13	—	—	23·6	0·050	0·0021	0·74	—
12	—	4·7 : 5·3 -	22	0·025	0·0012	0·41	—
14	—	5·0 : 5·0 -	32·5	0·025	0·00078	0·79	—
8-10	—	6·0 : 4·0 -	41	0·006	0·00015	0·76	—
—	—	—	—	—	—	—	—
—	—	—	100♂	0·048♂	0·00074♂	1·5♂	—
15-17	44	6·5 : 3·5 -1·8 : 8·2	69♀	0·069♀	0·001♀	1·06♀	—
10-12	28	5·5 : 4·5 -1·2 : 8·8	56·5♀	0·042♀	0·00092♀	0·85♀	—
10-12	30	5·5 : 4·5 -2·0 : 8·0	82♀	0·015♀	0·00018♀	1·15♀	—
7-9	26	6·6 : 3·4 -1·6 : 8·4	110♂	0·51♂	0·0047♂	5·1♂	—
—	—	—	66♀	0·31♀	0·0047♀	2·0♀	—
—	—	—	60	0·12	0·002	1·32	—
—	—	—	81	0·10	0·0013	1·15	—
—	—	—	95	0·048	0·00053	1·5	—
8	14	5·0 : 5·0 -2·9 : 7·1	172	0·095	0·00086	4·5	—
9	15	6·4 : 3·6 -2·6 : 7·4	36	0·018	0·0005	0·35	—
—	—	—	—	—	—	—	—
—	—	—	7·2	—	—	—	—
—	—	See Part 3	76	—	—	—	—
—	—	See Part 3	—	—	—	—	—
—	—	See Part 3	53	—	—	0	2·8
—	—	See Part 3	10	—	—	0	0·88
—	—	See Part 3	5	—	—	0	0·43
—	—	See Part 1	9·5	—	—	0	0·5
—	—	—	—	—	—	—	—
—	—	—	1·3	—	—	—	—
—	—	—	0·8	—	—	—	—
—	—	—	1·4	—	—	—	—
—	—	—	0·3	—	—	—	—

other groups for purposes of comparison. The species within each order are arranged in sequence of decreasing weight (the same species give slightly different values). Where the depth and width of a ring or segment (column 3) are relaxed, narcotized specimen, and those for *Peripatopsis* show the range of shape from the fully extended obtained as a result of many experiments, and those given on the left of column 5 show the numbers of legs (column 2); different specimens of the same size but slightly different weight and physiological state give figures

but *Glomeris* frequently will not perform a gait faster than (4·0 : 6·0). Animals which have been kept for some time in captivity or under abnormal temperature conditions may behave differently, and often use gaits with relatively longer back-strokes, as might be expected from the behaviour of captive centipedes (Part 3, pp. 134 and 151). The phase differences between successive legs which are most frequently employed are shown on the left side of column 5, Table I, expressed as the number of legs comprising each metachronal wave. The factors controlling phase differences have already been considered (p. 330).

Loading millipedes, either by saddling or by harnessing to sledges (see p. 302), calls forth the more powerful gaits with longer relative durations of backstroke, and therefore a larger proportion of the legs at each moment in the propulsive phase. The effects of saddling an *O. guineensis* weighing 20 gm. with loads of 70, 104 and 114 gm. are shown in Pl. 52, figs. 12, 13 and 14. The unloaded animal in fig. 11 performs gait (5·8 : 4·2) with about 12 legs per wave. A load of 70 gm. (fig. 12) calls forth a (4·3 : 5·7) gait with 20–22 legs per wave, a load of 104 gm. (fig. 13) lengthens the backstroke to gait (3·7 : 6·3), increasing the number of legs per wave to 22–24, and a load of 114 gm. (fig. 14) induces a yet more powerful gait of (2·9 : 7·1) with 25 legs per wave. The pressure from the saddles prevents the animals standing up on their legs as fully as in fig. 11, but the ventral surface is always held clear of the ground. A heavier loading can more easily be obtained by harnessing the millipedes to sledges of various weights, and as the load is increased, so the relative duration of the backstroke and the length of the wave increases. The loaded *Polydesmus* in Pl. 55, figs. 40 and 41 show gaits (2·2 : 7·8) and (1·6 : 8·4) compared with its free walking gaits of (6·6 : 3·4) to (5·5 : 4·5), Pls. 53, 54, figs. 22, 38 and 39, while the loaded and unloaded *Craspedosoma* (Pl. 53, figs. 20 and 21) show respectively gaits (2·3 : 7·7) and (5·3 : 4·7). *Polyzonium* shows gait (2·6 : 7·4) in Pl. 55, fig. 49 progressing against a load, compared with gait (6·4 : 3·6) seen in figs. 36 and 48. In *Glomeris marginata* the fastest unloaded runs show gait (5·7 : 4·3) as in Pl. 54, fig. 29, while gaits (1·0 : 9·0) and (1— : 9+) are shown in Pl. 54, figs. 30 and 31 when progressing against a load. The most powerful gaits which have been recorded under conditions of loading are entered on the left of column 6, Table I.

The phase differences between successive legs employed on fast free runs and when pulling a maximum load are shown on the left and right sides of column 5, Table I. The use of from 12–25 legs to a wave in *Ophistreptus guineensis*, for example, is correlated with the pattern of the gait (see p. 330) and the gait is determined by the power requirements of the animal. As many as 52 legs per wave have been seen in a loaded *Plusioporus sulcatus*, and smaller numbers in the British Juliformia with a smaller total number of legs. In the Nematophora as many as 26 legs and 44 legs per wave, out of the total of 50 legs, have been seen respectively in loaded *Craspedosoma* and *Polymicrodon*, and Löhner's photographs of slow and fast running *Lysiopetalum* show 7·5–8 rings (15–16 legs) per wave in the fast gait and about 10 rings (20 legs) in the slower one. Similarly a transition from 7 up to 26 legs per wave out of a total of 30–31 legs in the Polydesmoidea and one from 9 up to 15–22 legs per wave out of a total of 70 pairs of legs in *Polyzonium* is dependent upon the utilization of progressively more powerful gaits.

THE ANGLE OF SWING OF THE LEG.

In most Arthropoda it is not easy to record directly the variations in the angle of swing of the leg (Part 2, p. 105). The effects of changes in the angle of swing of the leg can be calculated for millipedes as for other Arthropods (see p. 336 and Part 2), but certain changes can be appreciated from the photographs. Text-figs. 5 c, f and i show that for any given number of legs in each group which are performing the forward swing, the length X is inversely proportional to the angle of swing of the leg. Taking groups of 9 legs in the forward swing in an *O. guineensis* 175 mm. long, the length X in gaits (5·8 : 4·2) to (5·4 : 4·6) is 4·5–5·5 mm. (fig. 11), but at gaits

(4·3 : 5·7) to (2·9 : 7·1) X is 7·5–10 mm. (figs. 12–14). This means that the angle of swing of the leg is smaller in the gaits with the longer relative durations of the backstroke (the more powerful gaits). However, at gait (6·7 : 3·3) (fig. 15) X is 8·1 mm. where 9 legs are off the ground, indicating that at this fastest gait a smaller angle of swing of the leg is used than in gaits near (6·0 : 4·0). A similar condition was found for *Peripatus*, where maximum speeds were sometimes obtained by the use of a 'top gear' gait, but with a smaller angle of swing of the leg than occurs at the fast speeds in 'middle gear' gaits (Part 1, p. 555). In the Polydesmoidea and Nematophora smaller angles of swing of the legs are used against a maximum load than when freely walking (see next section and Pl. 55, figs. 38 and 41). Species which are always slow in covering the ground may also show small angles of swing of the legs. Photographs in ventral view of *Cylindroiulus londinensis* walking on glass show an approximate angle of swing of the leg of 68°, while *Glomeris*, using a slower gait, shows an angle of 33–40°. In all groups of millipedes which have been examined the angle of swing of the leg is smaller in the more powerful gaits.

THE CONSTANCY OF THE FORWARD STROKE.

In any one species of millipede the range in the number of legs performing the forward stroke is small. In photographs of *Ophistreptus guineensis* the number is 6–9 while the propulsive groups show numbers of 5–18 legs. Out of 27 metachronal waves performed by this animal using a variety of gaits, 22 waves showed 7, 8 or 9 legs off the ground and the remainder either 6, 10 or 11 legs off the ground. The average of 8·7 legs in each group performing the forward stroke, although not maintained exactly, is advantageous; fewer legs lead to mechanical interference, and more leaves unnecessarily long unsupported gaps. A little crossing of the legs takes place on the forward stroke, when the legs are lifted up and over each other, as is seen in the photographs of *Plusioporus* and *Polydesmus* (Pl. 53, figs. 22 and 25); a smaller number of legs in each recovering group, which would shorten the distance X, would lead to mechanical interference. It is the need to maintain a constant form to the groups of legs performing the forward stroke (see consideration of the distance X on p. 330) that has led to the utilization of numbers of from 6 up to 44 legs in the propulsive groups of *Plusioporus sulcatus* and from 4 up to 18 legs in *O. guineensis*. The Nematophora are similar to the Juliformia in this respect. *Craspedosoma rawlinsi* usually shows groups comprising 5–7 legs off the ground, both when walking freely and when progressing against a maximum resistance (Pl. 53, figs. 20 and 21), and under these two circumstances the propulsive groups comprise 5–7 and up to 27 legs respectively. The legs of *Polymicrodon polydesmoides* are longer than those of *Craspedosoma* (see Table I, column 4) and, as might be expected, the necessity to maintain the distance X (see text-fig. 5) at a workable dimension has increased the numbers of legs in the recovery groups to 7–9 (Pl. 53, fig. 18) compared with *Craspedosoma*. Löhner's (1914) photographs of *Lysiopetalum illyricum* show 9–10 legs in the recovery groups when the animal was running fast and 6–7 when running slowly. *Polyzonium* usually shows 5 legs in each recovery group in all gaits (Pls. 54, 55, figs. 36, 48 and 49), a small number correlated with the shortness of the legs, and in *Blaniulus* it is the unusually long ring for a juliform that results in as few as 4–5 legs forming the recovery groups (Pl. 53, fig. 27).

In millipedes with fewer legs than in the above orders the constancy in number of legs performing the forward stroke in each wave holds only for free runs. In *Polydesmus* (Pl. 55, figs. 38 and 39) each group of legs performing the forward stroke usually numbers 4 or 5, although it may be 3 or 6, and there is little crossing over owing to the length of the rings (Pl. 53, fig. 22); in *Glomeris marginata* (Pl. 54, fig. 29) it is 2–4, 3 being the commonest number. However, when progressing against a resistance the smaller total number of legs present makes very long waves with numerous propulsive legs an impossibility. *Glomeris* with a total of 17 pairs of legs has not been seen to use more than 7 consecutive legs in the propulsive phase in

one wave, in contrast to from three to seven times than number so employed by the Juliformia (Table I, right side of column 5). There is a tendency in the Polydesmoidea and Oniscomorpha to employ as many of their legs in a propulsive state as possible. The angle of swing of the leg is often small, and the distance X can therefore be small also, so that fewer consecutive legs are needed in the forward stroke. *Polydesmus* progressing against a resistance may still show 4 legs in the recovery stroke, as in Pl. 55, fig. 40, where right legs 8–11 are off the ground and are followed by 11 or 12 propulsive legs, but in Pl. 55, fig. 41 the recovery group of legs is reduced to 1, left leg 8 is off the ground while legs 2–7 and 9–18 are propulsive. In the loaded *Glomeris* in Pl. 54, fig. 30 the recovery group is reduced from 3 to 1, leg 8 only being off the ground. The distance X is now non-existent, as in text-figs. 5 g and k, the tips of legs 7 and 9 being close together on the ground. In fig. 31 all legs are propulsive at the moment shown, three metachronal waves being represented by legs 1–6, 7–9 and 10–17. The absence of even one leg in the recovery phase results in the crossing of the propulsive legs at the beginning and end of each wave (see legs 6 and 7, and legs 9 and 10 as in text-figs. 5 k and n). This condition has not been found in any other millipede, where the propulsive legs do not cross, and is advantageous to the short bodied *Glomeris* in allowing all or almost all the legs which are present to push simultaneously, but their angles of swing must remain small, and progression becomes very slow.

PACE DURATION.

The stable character of the groups of legs performing the forward stroke has been noted above, and this uniformity extends also to the duration of the forward stroke, which is much less variable than that of the backstroke. In *O. guineensis* the forward stroke is executed in 0·32–0·46 sec. on unloaded runs and in 0·5–0·7 sec. on loaded runs, the slower strokes occurring with the heavier loads. The duration of the backstroke is usually 0·24–0·33 sec. on unloaded runs, and 1·2–1·5 sec. as the load is increased from 70 to 114 gm, becoming longer as the load is further increased. Pace durations in other large Juliformia, *Plusioporus sulcatus* and *Graphidostreptus judaicus* (Pl. 53, figs. 25 and 26) were not less than 0·7–0·8 sec. on unloaded runs. The smaller British *Cylindroiulus* species and *Schizophyllum sabulosum* (Pl. 52, figs. 9 and 10) can quicken the pace to 0·5–0·6 sec. and *Tachypodoiulus niger* and *Micropodoiulus scandinavius* to 0·45 sec. The shortest pace durations recorded for *Glomeris* and *Polyzonium* are 0·7 and 0·8 sec. respectively, and for the Polydesmoidea 0·4 to 0·5 sec., where the duration changes but little over a considerable speed range. *Polymerodon polydesmoides* and *Microchordeuma scutellare* readily shorten the pace to 0·3 sec. or less. The short pace durations of the larger Juliformia (which are less efficient at burrowing, see p. 344) and of the Nematophora make possible the fast running shown by these millipedes. Thus the pace durations of the Diplopoda can be a little shorter than in the Onychophora (Part 1) and are much longer than in the Chilopoda (Part 3) when both are moving fast.

SPEED.

Increase in speed tends to be accompanied by a decrease in the pace duration, by a decrease in the relative duration of the backstroke and by an increase in the angle of swing of the leg, as in other Arthropoda (Part 2, Table 1), but the correlations between these factors is not so regular as in fast running arthropods such as the Scolopendromorpha and anamorphic Chilopoda (Part 3). In *O. guineensis* the contributions to an increase in speed by these factors are roughly : decrease in pace duration 32 per cent, decrease in relative duration of the backstroke 23 per cent, and increase in angle of swing of the leg 45 per cent, for unloaded and loaded runs, giving a speed range of 10–40 mm.p.sec., but, as shown above, the fastest gaits are not performed at a maximum angle of swing of the leg. Owing to the variability of behaviour, these figures have a less precise significance than those given in Part 2, Table 1. However,

they indicate the relative importance of the three factors. An example of the variability of these correlations is shown by *O. guineensis*, where a pace duration of about 0·85 sec. is used by various gaits, giving stride lengths of 16–25 mm., together with the slowest and fastest speeds which are easily obtainable from unloaded animals. Bethe and Thorner (1933) noted a variability in performance by different individuals of the same species.

The type of performance frequently exhibited by the Juliformia can be illustrated by an *O. guineensis* 175 mm. long. When freely running a speed range of 20–45 mm.p.sec. is given by pace durations of 0·65–0·9 sec. with strides of 18–35 mm. by gaits ranging from (6·7 : 3·3) to (5·0 : 5·0); and when saddled with loads up to four times the body weight, the speeds were reduced to 8·5–10 mm.p.sec., the pace duration to 1·5–2·5 sec. and the stride to 15–21 mm. by gaits ranging from (4·0 : 6·0) to (2·9–7·1).

It will be noted that the stride length of a loaded run may exceed that on a faster unloaded one. In most Arthropoda, including insects, stride lengths have been found to decrease with decreasing speed and 'lower gears' and the gait can be ascertained from the track (Parts 1 and 3). The gaits of millipedes cannot always be ascertained from the track. When moving quickly by a fast gait the stride is long and the footmarks tend to show forward and inwardly directed flourishes, particularly if the legs are long, as occurs in the Chilopoda (Part 3, text-figs. 5 d and 11 c). As the speed decreases, so does the stride, but speeds of $\frac{3}{4}$ – $\frac{1}{2}$ of the maximum executed by a variety of gaits can give the same stride lengths. Tracks with short strides, and therefore very many marks per unit length, are made by slow runs in 'low gears'. The fairly long strides of millipedes in 'low gears' are due in part to the great increase in the pace duration (Part 1, p. 536) which is made possible by the possession of very many legs and a small phase difference between successive legs.

The maximum speeds shown by various juliform species do not differ greatly when allowance is made for size, although it is not possible to compare exactly the performance of species differing in both size and shape. The larger species, 175–104 mm. long, achieve up to 45 mm.p.sec., while the smaller British *Cylindroiulus* species, *Schizophyllum sabulosum* and *Tachypodoiulus niger*, all of about 25 mm., reach 8, 10 and 13 mm.p.sec. respectively, the latter species attaining 18 mm.p.sec. at a length of 40 mm. The longer legged species such as *Tachypodoiulus niger*, *Micropodoiulus scandinavius* and *Plusioporus sulcatus* are fleetier than the shorter legged ones, and the two former species also step quickly.

As might be expected, *Polyzonium* and *Glomeris* cover the ground but slowly, speeds of 1·7 and 4 mm.p.sec. being achieved respectively by 11 mm. specimens of these species, but on a basis of similar ring volumes *Polyzonium* is the faster (see Table II). *Glomeris* takes strides of little more than half the length of those of juliform species of similar ring volume.

The Polydesmoidea are much fleetier than the Juliformia. The maximum speeds achieved by *Polydesmus angustus*, *Tachypodoiulus niger*, *Cylindroiulus londinensis* var. *caeruleocinctus*, and *Glomeris marginata*, all weighing 0·08 gm., are 22, 13, 4·5 and 3·5 mm.p.sec. respectively. Comparisons between specimens of similar ring volume put the performance of these animals in the same order (Table II). In *Polydesmus* the pace duration may not change very much. A speed range of 11 to 22 mm.p.sec. in *P. angustus* can be achieved by almost the same gait, almost the same pace duration but considerable variation in the angle of swing of the leg. The great sexual differences in the adult of this species in both length and stoutness of the legs (Table I, column 4, Pl. 55, figs. 38 and 39 and text-figs. 2 e and f) result in sexual differences in performance. In bright light the female tends to run faster, using a shorter pace duration and shorter stride than the male, the most frequent figures for the male and female respectively being a pace duration of 0·5–0·6 and 0·4 sec., a stride of 8–8·5 and 6–8 mm. and a speed of 14–16 and 16–20 mm.p.sec. Both, however, on occasion can show the same maximum speed.

The Nematophora are fleet than the Polydesmoidea. An 18 mm. *Polymicrodon polydesmoides* achieves 20 mm.p.sec. compared with 22 mm.p.sec. by a 20 mm. *Polydesmus*, but taking animals for comparison with the same body weight or the same ring volume, *Polymicrodon* is 33–50 per cent faster than *Polydesmus*. The gait of *Polymicrodon* and its pace duration on free runs change more readily than they do in the Polydesmoidea. Alterations in the angle of swing of the legs are responsible for considerable changes in speed, but this factor is not of such dominating importance as in the Polydesmoidea. *Microchordeuma* is relatively fleet than *Polymicrodon*, an 8·5 mm. specimen achieving 14 mm.p.sec. Only one specimen of *Craspedosoma* has been obtained alive, and its speed of up to 5 mm.p.sec. was probably not maximal and its pace duration of 0·8 sec. may not have been minimal because the animal travelled into this country before being examined, and the related *Polymicrodon polydesmoides* does not always live well in captivity.

TABLE II.

	Relative powers of pushing by the legs	Relative speeds
Diplopoda		
Oniscomorpha	1	1
Juliformia	1	4–9
Colobognatha	1	2
Nematophora	2–3	26
Polydesmoidea	2–5	15
Onychophora	0	2·3
Chilopoda		
Geophilomorpha	0	4–18
Scolopendromorpha	0	95
Lithobiomorpha	0	126
Scutigeromorpha	0	220
Vertebrata		
Lizard	0·2	—
Mouse and Hamster	0·3	—

A summary of the relative speeds and pushing powers of millipedes, other Arthropoda and vertebrates. The performance of a *Glomeris marginata* has been taken as unity, and the pushing powers and speeds of other species of millipedes are based upon comparisons between animals of the same ring volume (see pp. 336, 340 and Table I). Comparisons with Peripatus and centipedes are based upon animals in which the volume of 2 segments equals that of a diplopodan diplo-segment. Comparisons between the lizard, mouse and millipedes are based on animals of similar body weight.

Thus Juliformia with the same segment volume as Peripatus (Table II, and Part 2, text-figs. 4 and 5) in 'low gears' progress a little faster than does Peripatus and three or four times as fast when using their faster gaits. The Oniscomorpha walk more slowly than Peripatus, while the Polydesmoidea are considerably faster, achieving about one and a half to twice the speeds of the Juliformia, according to the basis chosen for the comparison, and the Nematophora can be nearly twice as fast as the Polydesmoidea. However, it is not for speed that most millipedes are remarkable, although they have progressed beyond the Onychophoran stage in this respect, but for the pushing force which they can exert by their legs (see Table II).

LOCOMOTORY MOVEMENTS OF THE STERNITES.

In the Nematophora, Oniscomorpha and Colobognatha the sternites move backwards during the propulsive leg stroke and forwards during the recovery stroke,

relative to the tergites. The leg bases are closer together in the groups of legs performing the backstroke than in the groups swinging forwards. The median side of the leg base in *Glomeris* is dark in colour while the pedigerous membrane is white, and these dark marks in Pl. 53, fig. 17 are farther apart between legs 2–5, 9–12 and 15–16 than between legs 6–9 and 12–15. The propulsive legs are marked by dots. *Polymicrodon* (Pl. 54, fig. 28) similarly shows the bases of the propulsive legs to be closer together than those in the recovery phase. If these movements of the leg bases were due to an inability of the sternites or tracheal pouches to withstand the thrust exerted by the legs, the bases of the legs would lie closer together on the propulsive leg stroke. Since this disposition is not seen, it is concluded that the musculature already referred to (pp. 319, 323 and 324), and in particular the musculi apophyses sternales, by sliding the ventral elements forwards and backwards, provide a locomotory force additional to that given by the intrinsic and extrinsic leg muscles.

During the forward stroke of *Glomeris* successive tracheal pouches are pulled together and the leg bases are thereby approximated, the thin flexible membrane which separates them (text-fig. 4 c) becoming folded. At the same time the forward overlap of the laterally placed sternites is increased. In the Nematophora the tracheal pouches are similarly pulled together, but by a greater variety of muscles, and this movement results in sliding the median sternites, from which the legs originate, over one another from before backwards (text-fig. 2 o). As in the Juliformia, the sternites and tracheal pouches have an upward and anteriorly directed tilt, and this allows the sliding to take place. The sliding movement is executed without displacement of the tergites, which remain regular all along the body as in the Juliformia. In *Polyzonium* the short sternites are pulled together without much overlap.

The range of the sliding movement varies with the gait. In *Glomeris* walking freely the movement may cover 30 per cent of the length of the exposed part of the ring. In *Glomeris* when walking slowly and in the Nematophora the movement may be small; the median papilla on each sternite just anterior to the leg base shows clearly in *Craspedosoma* (Pl. 55, fig. 45); these papillae are more evenly spaced than are the leg bases in figs. 17 and 28. When the Nematophora, Oniscomorpha and Colobognatha are exerting themselves, either by running fast or progressing against a resistance, the range of movement is greater. Successive leg bases are brought almost as close together during the recovery stroke as in the spiral or 'pill' position. The forward drag on the ventral elements becomes less localized, and during the forward stroke the whole ring may be pulled forward ventrally, resulting in a marked dorsal humping of the body over the legs in the recovery stroke. Similarly, during the backstroke the ventral parts of the tergites are pulled posteriorly. The elaborate involvens muscles and the flexor inferus longus must aid this movement. The hump shown for *Polymicrodon* and *Craspedosoma* pulling a maximum load in Pl. 53, figs. 19 and 21 and two humps seen in Pl. 55, fig. 49 for *Polyzonium* travel forwards along the body. By this means the legs are brought forward as far as possible for the beginning of the backstroke. In *Glomeris* progressing against a resistance a marked humping may occur when the number of legs forming the recovery group is small. This is not shown in Pl. 54, fig. 30, although only one leg is off the ground, but there is a marked dorsal exposure of rings 6 and 7 in fig. 31 where one leg at a time will be raised from the ground. In this way a considerable amount of the ring musculature can be utilized at times to supplement the locomotory force supplied by the legs.

A dorsal humping over the groups of legs in the recovery stroke is shown in Clementi's figure (1912) of a julid. This humping can sometimes be seen in Juliformia and Nematophora when running fast, and in these orders and in the Polydesmoidea when progressing against a resistance, but the degree of humping is greatest in millipedes with free sternites. *Cylindroiulus* and *Polymicrodon* in Pls. 52, 53, figs. 10 and 18 show this humping; the ventral parts of the rings of *Cylindroiulus* are pulled forwards at the beginning of the backstroke and by the end of the backstroke the

sternal parts of the rings lie more posteriorly than they would do if the rings kept a regular alignment all along the body, as seen in most of the photographs of the Juliformia in side view on Pls. 52 and 53. The movements of the sternites of the Juliformia resemble those of the Nematophora but on a smaller scale, and presumably supplement the locomotory force in a similar but smaller way. A more marked utilization of the body muscles in this manner for locomotion is seen in the Juliformia progressing against a resistance.

Similar principles are employed by the larvae of sawflies and of Lepidoptera, where the legs are brought forwards during the recovery phase by the body musculature. The soft body often does not hump more markedly than in the Nematophora, but the leg movements may be reduced almost to one of intermittent fixation. The bulk of the forward progression is then achieved by the alternate humping and straightening of the body (see a subsequent Part). This similarity between soft skinned larvae of insects and certain Diplopoda has no phylogenetic significance.

PUSHING POWER.

The maximum pulling force that can be exerted by millipedes harnessed to a sledge has been recorded (p. 302). Presumably the animals can push against a resistance with a force similar to that exerted in pulling a load, since no telescoping of the body segments usually occurs. In Table I, column 7 the maximum pulling force which can be exerted by the legs (f) is divided by the body weight (w), so giving a basis of comparison between species. As shown below, the size of a millipede affects its pushing power, so that comparisons between species with unlike segment numbers may be based on similar size or weight of either the whole animal or of a single diplo-segment.

Taking body weight as the basis for comparison, representatives of the several orders show their relative powers as pushing animals to be: Oniscomorpha, 1; Juliformia, 1.8; Nematophora, 3.1; and Polydesmoidea 6.5 (see entries in Table I for *Glomeris*, *Cylindroiulus* and *Polydesmus*, all of about weight 0.08 gm., *Craspedosoma* of 0.025 gm., *Cylindroiulus* of 0.02 gm. and *Polydesmus* of 0.015 gm., and taking the entry for *Glomeris* in column 7 as unity). Probably a better basis of comparison is that of common diplo-segment volume. A *Glomeris* and a *Cylindroiulus* with ring volumes of 6.5 and 6.2 cu. mm. respectively have roughly the same (f/w). A *Craspedosoma* ring volume of 0.97 cu. mm. corresponds with that of an animal in between *Cylindroiulus punctatus* and *C. londinensis* of ring volumes 0.54 and 1.5 cu. mm. and such a juliform millipede would be expected to have an (f/w) of between 32 and 23, as indeed it does. *Polydesmus* and *Micropodoiulus* of ring volume 1.4 cu. mm. roughly correspond with *Polymicronod* of 1.2 cu. mm., and *Blaniulus* is close to *Microchordeuma*. On this basis the Oniscomorpha and *Polyzonium* approximately equal the Juliformia in pushing power, and if this is taken as 1 the pushing power of the Nematophora becomes 2 and that of the Polydesmoidea 2.5. On either basis the Polydesmoidea and Nematophora are very much more powerful than the other orders (Table II).

It is this ability to push against a resistance which distinguishes the Diplopoda from other Myriapoda and makes possible their particular methods of burrowing. The Onychophora and Chilopoda when similarly harnessed to sledges make no attempt to pull a load by the motive force of the legs. They hold on with the legs and intermittently shift the load by the contraction of the longitudinal body muscles ; the anterior end of the animal then walks forwards as far as the extensibility of the body permits, and holds on again for the next pull. The pulling force which is exerted in this way by the body muscles of *Peripatopsis*, *Cryptops* and *Lithobius* is less than the force put out by the legs in millipedes of comparable size (see Table I, columns 2 and 7), and under normal circumstances the former animals do not push. Peripatus can change its shape and squeeze through very narrow places, but the skin is covered everywhere by papillae, each bearing an exposed sensory

spine, and the animal could hardly attempt to push by its general surface. The geophilomorph *Stigmatogaster* burrows by exerting a pressure through the body surface against the soil, due to the longitudinal contraction of body muscles (Part 3). The pulling force (Table I, columns 2 and 7) which it can exert is almost as powerful as that of *Polydesmus*, the Polydesmoidea being the most powerful of millipedes, but the force is mediated by the body muscles in the centipede and by the legs in the millipede.

The pushing force of the Juliformia and Oniscomorpha is exerted mainly by the head end, and thus the push exerted per sq. mm. of transverse sectional area of the body becomes of importance to the animals and serves also as a basis of comparison between species (Table I, column 9). For the 'flat backed' millipedes (Nematophora and Polydesmoidea) and Colobognatha this figure has a less real significance, since the animals exert their push mainly by the dorsal surface and not by the anterior end. A figure is entered for the Onychophora and Chilopoda in column 10 for comparative purposes, but only that relating to *Stigmatogaster* is significant in the normal life of the animals.

The total pushing power of a millipede, and its pushing power relative to the transverse sectional area of the body, depends upon (1) the size and (2) the shape of the rings, (3) the size and form of the legs relative to the ring and (4) the number of rings comprising the body. Effects of changes in these factors will now be considered.

EFFECTS OF LEGS OF DIFFERENT TYPES, AND OF HEAVINESS OF BUILD OF THE BODY, ON PUSHING POWER, SPEED, AND HABITS.

Rings of equal volumes from different millipedes differ in the length of their legs, and where the legs are of similar shape, the longer the leg the more powerful is the pushing force usually exerted by the ring. The length of the leg relative to the diplo-segment which bears it is given in Table I, column 4 expressed as (leg length/ $\sqrt[3]{\text{ring volume}}$) in order to indicate comparisons between animals with differently shaped rings. Where two animals have roughly the same ring size, the larger values in column 4 are correlated with a larger pulling, and presumably pushing, force being exerted by each ring.

Compare for example the figures in column 4 and left side of column 8 for *C. londinensis* and *T. niger*, both 38 mm. long. The ring volume of *T. niger* is less than that of *C. londinensis*, yet a ring of *T. niger*, provided with longer legs, puts out the greater pushing force. *Polymicrodon* with a slightly smaller ring volume (1.2 cu.mm.) and slender, longer legs puts out a greater force per ring than does *Cylindroiulus* of ring volume 1.5 cu.mm. The two sexes of *Polydesmus angustus* show marked dimorphism in legs (Pl. 55, figs. 38 and 39) and a ring of the longer and stouter legged male puts out a greater force than does that of the female. The sexes of *Polymicrodon* differ similarly in this respect (Table I). The legs of *Polydesmus* are stouter than those of *Polymicrodon*, although a little shorter, and the pushing power of a 1.4 cu.mm. ring of *Polydesmus* greatly exceeds that of an adult *Polymicrodon*. The ring volumes of *Microchordeuma* and of *Blaniulus* are almost equal, but the longer legged *Microchordeuma* can put out two and a half times the pushing force of a *Blaniulus* ring. The increase in pushing power which results from longer legs is further illustrated by text-fig. 6 (see p. 344).

Thus the great pushing power of a ring of *Polydesmus* appears to be correlated with the possession of long stout limbs. The pushing power of a ring of the Nematophora, which is intermediate between that of the Polydesmoidea and Juliformia, is associated with legs which are longer than in the Juliformia but less stout than in the Polydesmoidea, and with the utilization of a locomotory force originating in the muscles which slide the sternites, as well as that supplied by the limb muscles.

Millipedes can be found showing similar ring volumes and much the same general shapes, but with rings of markedly different weights. *Micropodoiulus scandinavius* and *Cylindroiulus londinensis* of ring volumes 1.4 and 1.5 cu.mm. respectively, and

Polymicrodon polydesmoides and a partly grown *Polydesmus angustus* of ring volumes 1.2 and 1.4 cu.mm. respectively are examples (see Table I, column 1). In each of these pairs the animals with the heavier rings (*Cylindroiulus* and *Polydesmus*) put out the greater pushing force per ring (left side of column 8), but those with the lighter rings (*Micropodoiulus* and *Polymicrodon*) run faster and step more quickly (p. 337). *Micropodoiulus* and *Blaniulus* are lighter per unit volume than the other juliform species entered in Table I and the pushing power of their rings is relatively less; *Micropodoiulus* shows an (f/w) appropriate to its size, but it exerts only 0.4 gm. per sq. mm. of transverse sectional area, while *Blaniulus* exerts an average total pushing power but by means of an unusually large number of rings (see column 9). It is noteworthy that *Micropodoiulus* inhabits litter and does not burrow freely as do the British Juliformia, which exert forces of about 0.7–0.8 gm. per sq. mm. of transverse sectional body area (see column 9). It seems probable that any increase in pushing power gained by lengthening and strengthening the leg and increasing the weight of the skeleton is achieved at the expense of fleetness, just as a cart-horse achieves power while a race-horse achieves speed. A combination of speed and power in millipedes, as in other animals, appears to be a compromise.

The length of leg in juliform millipedes is restricted by their burrowing habit. In pushing through soil or leaf mould the legs operate in a ventral space below the body, kept clear by their action. When they do not project beyond the lateral body wall they will encounter least hindrance to their movements, and will derive a considerable amount of protection from the body. In most species the legs project only just beyond the side of the body (Pl. 53, fig. 23 and text-fig. 7 h), up to a quarter of the diameter of the animal, and much less than in *Plusioporus* (Pl. 53, fig. 24), which probably lives more openly (see p. 345), and in many species they do not project at all, as in *Poratophilus* (text-fig. 3 d) and in *Archispirostreptus* (see Lankester's (1904) drawing in ventral view). The mid-ventral origin of the legs allows a maximum length with the minimum of lateral projection. The longest and shortest legged species which have been examined are *Plusioporus sulcatus* (Pl. 53, figs. 24 and 25) and *Poratophilus punctatus* (text-fig. 3 d) leg length/ $\sqrt[3]{\text{ring volume}}$ 1.7 and 0.7 respectively (see Table 1, column 4). Rings which are short and wide can carry a longer leg without undue projection than can rings of equal volume which are long and narrow. Text-fig. 7 d, l, shows a transverse section of a diplo-segment of *Tachypodoiulus* with appended legs, and those in text-figs. 7 a, l, c, l and g, l show sections of diplo-segments (or a pair of segments in text-fig. 7 a, l) with similar volumes but different shapes, as in the animals shown in text-figs. 7 a, c, d and g, the legs, the associated muscles and tracheal pouches in all being the same as in *Tachypodoiulus*. An animal as in text-fig. 7 a, l could not burrow effectively because the legs project too far. The proportions of the ring in text-fig. 7 c, l are those of *Blaniulus guttulatus*, and it is unlikely that *Blaniulus* could carry a leg as in text-fig. 7 c, l and still burrow; the legs of *Blaniulus* are relatively about 30 per cent shorter, which gives a usual amount of lateral projection. The legs in text-fig. 7 g, l derive more protection from the body than do those of *Tachypodoiulus*. The maximum degree of projection of the leg in Juliformia, which burrow well, does not appear to be greater than that of *Cylindroiulus* (text-fig. 7 h), where the (leg length/ $\sqrt[3]{\text{ring volume}}$) is 1.3. The figure for *Tachypodoiulus* is 1.6, nearly as great as in *Plusioporus*. It is significant that *Tachypodoiulus* burrows least of British Juliformia, being found under stones, bark, and loose material and never deep in the soil. It is probable that *Tachypodoiulus* has exceeded the leg length compatible with easy burrowing, and, as its name implies, this 'fleet footed' millipede has taken to more open habits. The Nematophora Lysiopetaloidae have not been obtained alive, and it is possible that some may be able to burrow with even longer legs than *Plusioporus* and *Tachypodoiulus* because of different leg morphology (see p. 362).

The legs in the Oniscomorpha, although resembling those of the Juliformia in length (Table I, column 4), are flexed in such a way that they do not project beyond the sides of the body, the ventro-lateral extensions of the tergites boxing them in. No lateral projections hinder burrowing (text-fig. 4 d and Pl. 54, figs. 29–33). A ring of *Glomeris* is about as powerful as one of a juliform millipede of similar volume and leg length. The angle of swing of the leg in *Glomeris* is small, and the power exerted by the leg is associated with its considerable dorso-ventral thickness (a limb flattened in the transverse plane is necessary to permit a close dorso-ventral flexure), and with the locomotory force provided by the musculi apophyses sternales and other muscles. In the Colobognatha also this extra locomotory force is sufficient to give a pushing power per ring of much the same order as in the Juliformia, although the legs are short (Table I, column 4).

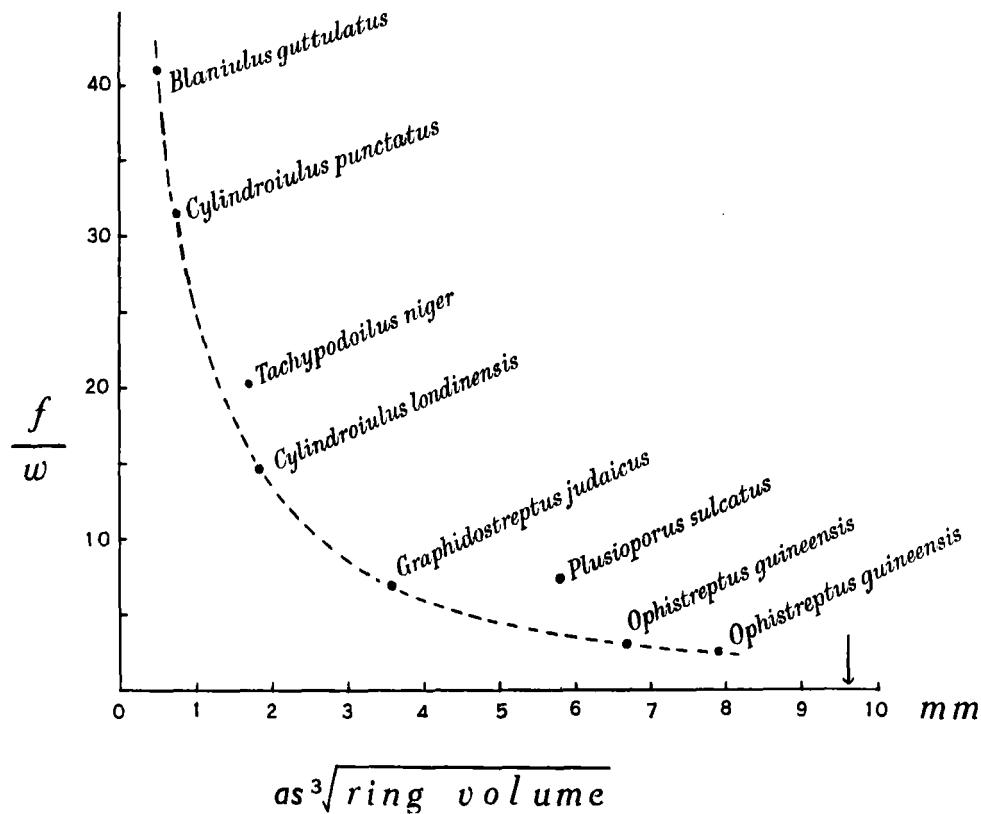
The long legs and projecting keels of the Polydesmoidea and Nematophora Chordeumoidea make burrowing into compact soil impossible. These features are associated with pushing by the 'flat back' into woodland litter, decaying stumps and under bark (p. 327). The area of application of the push by the back is much greater than it is in the Juliformia when pushing by the head, and the total force generated by the legs of the Nematophora and Polydesmoidea is suitably greater. In a resting *Polymicrodon* or *Polydesmus* the legs are brought close up to the sides of the body and under the keels (text-fig. 2 f, dotted line), unlike the position shown by the continuous line and by running animals in Pl. 55, figs. 38 and 39. A backward tilt of the legs brings them completely under cover of the keels and then they are invisible in dorsal view. It is probable that the legs are held close in to the body under cover of the keels when the animals are pushing with the back. The laterally directed origin of the legs and spiracles in *Polydesmus*, and the rigidity of the ring, render these animals particularly well suited to push themselves into cracks which are narrow in one plane. The nematophoran stance preserves the ventral air space supplying the spiracles (text-fig. 2 p) as in other groups of millipedes, excluding the Polydesmoidea, and the Nematophora, although powerful, would not be expected to be so adept at opening cracks as the Polydesmoidea. The peculiarities of the legs and the habits of the Lysiopetaloidae are considered on p. 361.

The pulling force exerted by two beetles is also entered in Table I. *Helops laevioctostriatus* can be found along with Juliformia deep in leaf mould near decaying stumps, and the pushing force which it can exert (Table I, column 7) is greater than that of Juliformia or *Stigmatogaster* of the same body weight and is of the same order as in *Polydesmus*. *Helops* is, however, shorter and wider than the Juliformia and probably exerts about the same order of push per unit of transverse sectional area. The violet ground beetle (*Cabarus violaceus*) is larger, with relatively longer legs, and does not penetrate so deeply into leaf mould, and the figure in column 7 is smaller than in the Juliformia. Presumably the long legs of *Cabarus* hinder deep burrowing, as do those of the Polydesmoidea, and the length of leg confers speed but not power to this beetle.

THE EFFECTS OF RING SIZE ON PUSHING POWER.

It can be seen from Table I, columns 1, 7 and 8, that as the size of a juliform millipede becomes larger, so the weight which is borne by each ring increases relative to the pushing force which can be exerted by that ring. Such a relationship is to be expected. Since the pulling force of the limb muscles is roughly proportional to their sectional area, and the weight of the ring is proportional to its volume, increase in size results in a greater proportion of the force exerted by the legs being utilized in carrying the weight of the ring, leaving a smaller amount available for pushing against a resistance. The effect of ring size on the pushing power of a ring is shown in text-fig. 6 where the coordinates give the pulling force exerted by one ring/weight of one ring (f/w), and the $\sqrt[3]{}$ ring volume. The dotted line unites points for species in which the relative leg length (see Table I, column 4) does not differ greatly. The

higher values for (f/w) for *Tachypodoiulus* and *Plusioporus* are related to the relatively greater lengths of their legs (Table I, column 4). A comparable curve for the Polydesmoidea lies very much farther from the base line because their (f/w) is greater, and the points for *Glomeris* of various sizes lie on or just below the line uniting points for the Juliformia.



TEXT-FIG. 6.

Shows the effect of size on the pushing power of millipedes. The $\frac{\sqrt[3]{\text{ring volume}}}{\text{body weight}}$

is plotted against the $\sqrt[3]{\text{ring volume}}$, and the points for juliform species with approximately comparable leg length (see Table I, column 7) are joined by the dotted line. The greater power of *Tachypodoiulus* and *Plusioporus* is correlated with their longer legs.

The range of size of the millipedes shown in text-fig. 6 is only slightly less than that of all existing juliform species. Ring volumes considerably less than that of *Blaniulus* do not exist, and an arrow shows the size of the largest specimen in the British Museum. Clearly the data for living Juliformia lie in the middle section of the curve, with ($\sqrt[3]{\text{volume}}$) of 0.5–9.5 mm., and not at the extremities. Moreover the existing species probably cover the size range over which this type of animal may be expected to be efficient.

The push of 0.32 and 0.17 gm. which is exerted per sq. mm. of transverse sectional body area by the two largest specimens, both *O. guineensis*, is considerably less than that exerted by the other species in Table I, column 9 and text-fig. 6, where the values are 0.66–1.5 gm. per sq. mm., except for the very lightly built *Micropodoiulus*, which burrows little (see above, p. 342). These values depend upon the shape and

number of the rings comprising the body (see below) as well as upon the factors under consideration. *O. guineensis* burrows well in soft, loose soil, but in compact soil the animal remains on the surface. Mr. L. C. Bushby of the London Zoo also notes that the largest millipedes in captivity remain on the soil surface or hide under bark. It is probable that *O. guineensis* is nearing the upper limit of size at which effective burrowing is possible. The largest millipede in the British Museum collections, an unidentified female 254 mm. in length of approximately similar form to *O. guineensis*, but with rings about 4·5 mm. long and 19 mm. deep, would have an (*f/w*) of about 2, that of *O. guineensis* being about 3 (text-fig. 6). This large millipede must therefore have been an even less able burrower than *O. guineensis*. Millipedes nearing 20 mm. in depth are few, and since their powers of burrowing must be poor except in very soft soil, it seems probable that they are near the upper size limit (see also p. 346). Mr. J. C. Battersby has collected the larger Spirostreptomorpha crawling about on the branches of trees in Kenya. Under sufficiently humid conditions a large, armoured millipede might well take to an exposed habit when its size renders its powers of burrowing inefficient. Moreover, the abundance of the discharge from the stink glands (see text-fig. 3, *s.g.*) is relatively greater in these millipedes, when the repugnant fluid is said to be sprayed out to a distance of several inches, than in the smaller British species. Some native peoples avoid walking near the large millipedes, believing that their secretions may cause blindness. The toxicity of the discharge does not appear to have been studied, but these secretions are known to burn holes in textiles. There are many factors which limit large size in arthropods, such as tracheal respiration and moulting, but the power which can be put out by the legs is alone sufficient to restrict increase in size in millipedes.

It is also possible that *Blaniulus guttulatus* is near the lower ring size for effective burrowing by the bulldozer method. Although the ratio (*f/w*) increases steeply with a decrease in size of the ring in the smaller millipedes, the area of application of the pushing force decreases. Soil particles of any given size will be less easily shifted when the site of application of the push is very small. Thus very minute millipedes employing the bulldozer method of burrowing might not be expected to exist. *Blaniulus* differs from the larger millipedes in its marked habit of readily flexing the body (see p. 310 and text-fig. 2 *j-m*), although the shape of the rings (Table I, column 3) renders the body less capable of acute bending than in most juliform species (see p. 311). *Blaniulus* appears to move through the soil or between obstacles in a zig-zag manner, selecting its path very freely. The 'fatter' larger millipedes are not so ready to twist and turn, and as far as is possible hold their bodies along a straight course, a procedure most suitable for pushing. The long narrow snake-like body of the 'spotted snake' millipedes contrasts with that of the larger forms, and may reflect a desirability of following the path of least resistance when small size renders the bulldozer method less effective.

Similar effects of size may be expected in other orders, although sufficient comparative data have not been obtained in illustration.

EFFECTS OF RING SHAPE AND RING NUMBER ON PUSHING POWER.

The majority of millipedes show a general similarity in their body proportions. *Ophistreptus*, *Cylindroiulus*, *Polymicrodon* and *Polydesmus*, for example, are roughly alike in overall shape, *Polymicrodon* being relatively longer and thinner than the others, yet they possess respectively about 60, 40, 30 and 20 trunk rings (Pls. 52–55, figs. 10, 11, 18, 22, 28 and 38). The majority of juliform millipedes show a body length between 9 and 14 times the depth. This figure is 8 for the short *Poratophilus punctatus*, while for *Graphidostreptus judaicus* and *Blaniulus guttulatus* it is 19 and 40 respectively; both are exceptionally long 'thin' animals (Pl. 53, figs. 26 and 27, the *Blaniulus* shown is a young specimen; the adult is a quarter as long again with 12 more rings). That there must be some general serviceability in a body that is neither extremely long nor short is shown by the many animals which approximate

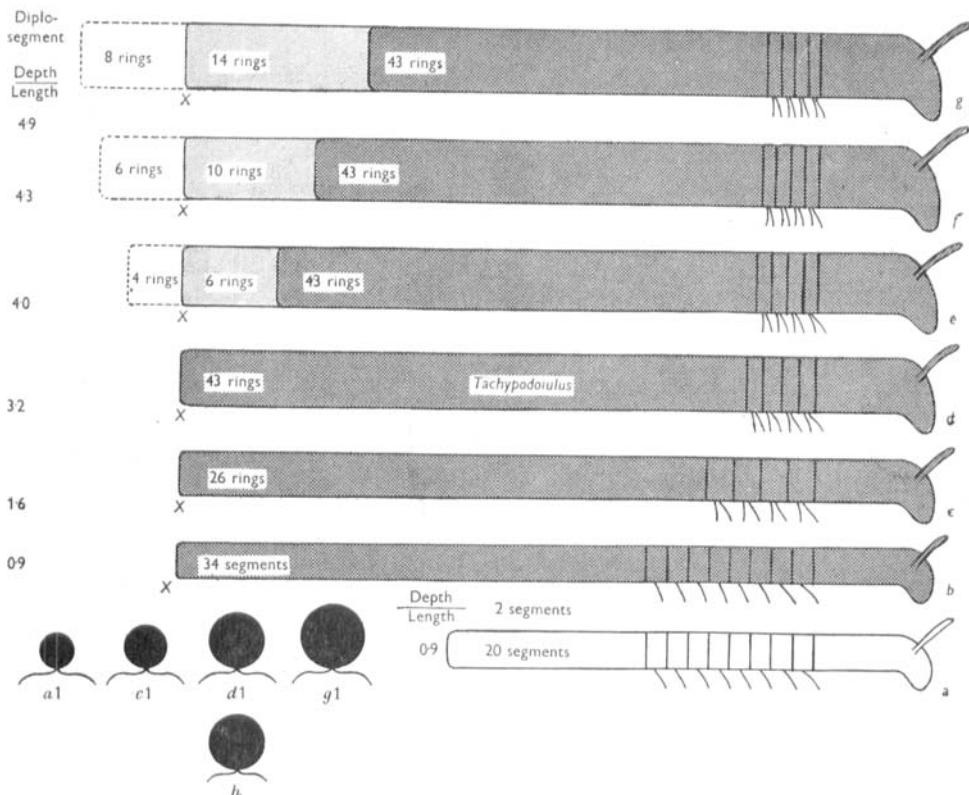
to this shape, and the shortness of *Glomeris* and the snake-like proportions of *Blaniulus* appear to be associated with special habits and with size.

The number of rings possessed by a millipede will affect the pushing power which can be exerted by the whole animal. The push which can be transmitted to the head end by each of the almost equal sized rings of a 38 mm. *Tachypodoiulus* and of a 10.5 mm. *Glomeris* is 0.12–0.13 gm., but the 43 leg-bearing rings of *Tachypodoiulus* produce four times the push per sq. mm. of transverse sectional body area as can be produced by the 10 rings of *Glomeris* (Table I, column 9). The ring volumes of *Plusioporus sulcatus* and *Poratophilus punctatus* are almost equal, but the former possesses more powerful legs, less deep rings and more of them (text-fig. 3 and Pl. 53, figs. 24 and 25), and the high figure for its pushing power (Table I, column 9) would not be expected to be given by *Poratophilus*. However, the latter species was collected from shallow excavations in the soil close against the under side of very large stones near Grahamstown, South Africa, so that the push which can be exerted (which has not been ascertained) must be sufficient for the animal to gain the protection of such sites.

The long body of *Graphidostreptus judaicus*, possessing about 10 or more rings additional to the numbers commonly present in the larger Juliformia (see below), exerts about twice the push per unit of transverse sectional area of the body as do other Juliformia shown in Table I, column 9, excepting the long legged *Plusioporus sulcatus*. However, if pushing power is advantageous, its attainment by unlimited addition of rings to the body appears to be unserviceable, since so few Juliformia other than Blaniulidae show bodies as long as *G. judaicus*. The habits of this Palestinian species are not known in detail.

Text-fig. 7 shows more exactly how the pushing power of a millipede is effected by the shape and the number of its rings. *T. niger* is indicated diagrammatically in text-fig. 7 d. If this animal merely became larger with no other alterations, its pushing power per unit of transverse sectional area would decrease (see previous section). If, however, the rings carry similar legs and maintain the same volume but become deeper and shorter, as in text-fig. 7 e, the original 43 rings would form a shorter body possessing a weaker pushing power per unit of transverse sectional area. The original pushing power per unit of transverse sectional area could be restored by adding 6 rings, so making the body as long as that of *Tachypodoiulus*, but if the original overall shape was also restored, a further 4 rings would be required, and such an animal would exert a greater push per unit of transverse sectional area than *Tachypodoiulus*. Text-figs. 7 f and g show the further effects of deepening and shortening the rings. The limbs in all are equal in length, and all are associated with similar sized muscles and are assumed to put out an equal pushing force. As the rings deepen, the original (stippled) 43 take up a shorter body length, elongation to X by additional rings restores the original pushing power, and elongation to the extent shown by the dotted line restores the original overall body proportions by the addition of 6 or 8 rings. The (f/w) of each ring will be the same as for *Tachypodoiulus*, and the segments present to the left of X will provide an additional push per unit of transverse sectional area of the animals in proportion to their number. Thus the maintenance of a constant overall shape, combined with shortening and deepening of the rings, the ring volume and leg length remaining constant, will increase the pushing power per unit of transverse sectional area of the millipede.

It has been shown above how increase in size of a ring leads to inadequate pushing power. Adequate burrowing power may be expected to be maintained with increase in ring size if the latter is accompanied by a shortening and a deepening of the rings and by an increase in their number. It is significant that the larger species of juliform millipedes possess shorter, deeper rings and more of them than the smaller species. The British species, excluding the Blaniulidae, are commonly under 40 mm. in length and 3 mm. in depth and possess less than 48 leg-bearing rings, the (depth/length) of which is 2.9–3.6. An inspection of a sample of the British Museum collections



TEXT-FIG. 7.

Diagrams showing (1) how an increase in pushing power for burrowing will be obtained by the transformation of a generalized arthropod into a diplopod by alterations in the proportions and in the number of its segments, the leg and its associated segment volume remaining constant; (2) the effects of changes in shape and in number of the diplo-segments of a diplopod on the pushing power of the animal and (3) how the shape of the ring determines the maximum length of leg which is practicable for a burrowing habit.

Figs. a-g : ring (diplo-segment) volume constant at 5.3 c.mm. as in *Tachypodoiulus niger* 38 mm. long, legs equal in length and assumed to have equal power. The eight segments or four diplo-segments drawn are of equal volume in each figure.

'X' shows the hinder limit of the body needed for each type of animal to exert the same pushing force per sq. mm. of transverse sectional area as is exerted by *Tachypodoiulus niger* (0.8 gm.); this body length is lightly stippled. A body longer than 'X' gives more pushing force, and one shorter than 'X' gives less. The heavily stippled parts of figs. d-g show the extent of 43 diplo-segments. The lightly stippled parts of figs. d-g show the additional rings (diplo-segments) needed to provide a pushing force of 0.82 gm. per sq. mm. of transverse sectional area, and the parts of the body enclosed by the dotted lines in figs. e-g show the extra rings needed to give the animals the same overall proportions as in *Tachypodoiulus niger*, fig. d.

Fig. a. A hypothetical arthropod without diplo-segments, each segment possesses a volume which is half that of the diplo-segment of *T. niger*, fig. d. The shape of the segments is that of Peripatus executing a 'bottom gear' gait. The overall shape is the same as *T. niger*. The pushing power per sq. mm. of transverse sectional area would be 0.5 gm.

Fig. b. A hypothetical arthropod with segments shaped as in fig. a but in number sufficient to give a pushing force per sq. mm. of transverse sectional area of 0.82 mm., that of *T. niger*.

Fig. c. Hypothetical animal with diplo-segments (similar to the ring proportions of *B. guttulatus*, but larger). The body with 26 rings possesses the same pushing power per sq. mm. of transverse sectional body area as *T. niger*.

Figs. a1, c1, d1 and g1 show transverse sections of the animals shown in figs. a, c, d and g, to illustrate the degrees of projection of the legs which are all equal in length (that of *T. niger*).

Fig. h. Transverse section of *Cylindroiulus londinensis* to show the shorter leg.

shows that species over 115 mm. in length possess 50–66 leg-bearing rings with a (depth/length) of 3·7–5·1, the majority of the sample examined being over 4·2. Specimens of the four largest species, the undescribed largest specimen, *Archistreptus dodsoni*, *Spirabolus cupulifer* and *Ophistreptus guineensis* are respectively 254, 225, 175 and 175 mm. long, and possess 65, 66, 51 and 60 leg-bearing rings with (depth/length) of 4·8, 4·5, 4·4 and 5·1. Species differ in the finer details of their habits and habitats, and therefore in their needs, and there is no exact correlation between size and shape of the rings.

The length of a ring is correlated to some extent with that of the leg. A wide ring allows a longer leg than a narrow ring in burrowers (p. 342). *Plusioporus* (Table I), from its size, might be expected to possess a shorter ring, but the length of its long leg appears to make a very short ring unsuitable, because long legs very close together will cross over on the forward stroke unless the phase difference between successive legs can be very small. Similarly the longer ring of *T. niger* compared with the larger British *Juliformia* is related to the longer leg.

The figures given in Table 1, column 7 show a regular correlation with ring size, as demonstrated by text-fig. 6, but the figures in column 9 are irregular and do not form an even series and have a smaller spread. The irregularity is presumably due to the variations in shape and number of the rings (columns 1 and 2), and to the relative length and strength of the legs (column 4), and were it not for the trend towards increase in ring number and the leg irregularities, the values in column 9 would steadily decrease from below upwards. The small difference in the pushing power per unit of sectional body area for the two species of *Cylindroiulus*, *T. niger* and *B. guttulatus* representing a size range of 0·007 to 0·34 gm. is striking. The legs of *Blaniulus* must, however, be relatively less efficient than those of the other species.

If the performance of other large species resembles that of *Ophistreptus*, the falling off in the pushing power suggests that beyond a ring volume lying roughly between 200 and 300 cu.mm. satisfactory adjustments of ring shape and number can no longer be made. The maintenance of adequate burrowing power with increase in ring size by a shortening and deepening of the rings of the body, and by an increase in this number, cannot be carried too far. Musculature can only be inserted upon less than half of the tergite length, and shortening of the rings brings difficulties in flexure of the ventral region (p. 311 and below). Thus a limit is set to size increase for reasons other than those mentioned in the last section.

THE EVOLUTION OF THE DIPLO-SEGMENT.

It is probable from what has already been said that an ancestral arthropod adopting a habit of pushing its way into leaf mould must initially have had short legs, not much longer than those of *Peripatus* (see Part 2, text-fig. 1), which did not project far beyond the sides of the body. The animal could have become a more efficient pusher by shortening and deepening its segments and increasing their number, at the same time maintaining the same overall shape (p. 346). With increasing depth and breadth of a segment, and a shift of the bases of the legs to a mid-ventral position, a longer leg could have been carried without much projection (p. 342), and with increase in leg length and in segment number giving greater pushing power, a smooth hard exterior and incompressible intersegmental joints must also have been evolved.

A progressive shortening, deepening and increase in segment number in the ancestors of millipedes can have advanced their efficiency in burrowing, but such a tendency must have been halted by at least two factors: (1) the practicability of short segments, and (2) the need to maintain a suitable, but not excessive, degree of flexibility of the body. The comparison between the powers of lateral flexure of *Blaniulus* and *Ophistreptus* (p. 311, text-fig. 2 m and n) shows that shorter rings increase the acuteness of the animal's lateral bending, but leads to difficulties by

restricting the space for muscle insertions on the tergites and for the accommodation of tracheal pouches and limb musculature in an acute ventral flexure. Reference to text-figs. 3 and 7 *d-g* suggests that single segments of half the length of the diplo-segments shown might be impracticable. Ball and socket joints of the juliform type could scarcely be devised so close together, and reference to the plates shows that the two or three anterior rings with one pair of limbs are never as short proportionately as half the length of the diplo-segments. If the components of diplo-segments were unfused, the body would be needlessly flexible; a sufficiency of mobility is essential, but all flexures at the joints must be firmly held by muscles when a push is transmitted to the head end, and excessive flexibility is unsuitable for a burrowing millipede.

A fusion together of short deep segments in pairs in a millipede ancestor would overcome the limitations just mentioned. An animal may be postulated (text-fig. 7 *a*) with an overall shape and leg length as in *Tachypodoiulus*, with a segment volume half that of the diplo-segment of *Tachypodoiulus*, and the shape of the segment the same as that seen in *Peripatus* executing a powerful 'bottom gear' gait; 20 such segments are needed to give the same overall shape as that of *Tachypodoiulus*. The pushing power per unit of transverse sectional area of *Tachypodoiulus* (fig. 7 *d*) would be 70 per cent greater than that of the animal in fig. 7 *a*, but if the latter burrowed, it would have to possess much shorter legs, projecting less far than in figs. 7 *a* and *a1*, and its pushing power would be very much less. Text-fig. 7 *b* shows the effect of adding segments to the body without altering their shape, sufficient in number to attain the same pushing power per unit of sectional area as in *Tachypodoiulus*. A long thin animal, 22 times as long as it is deep, results and this is unlike the majority of millipedes in shape (see above, p. 345). In text-fig. 7 *c* another hypothetical animal is shown with diplo-segments of the same shape as are present in *Blaniulus* but of double the volume of the single segments in figs. 7 *a* and *b*. The number of rings required to give the same pushing power as *Tachypodoiulus* is 26, a smaller number than present in most juliform millipedes, and except for the Blaniulidae, this hypothetical creature, which is 18 times longer than it is deep, is longer and thinner than most millipedes. In order to maintain the same overall shape and attain a pushing power equal to that of *Tachypodoiulus*, the segments of the hypothetical beast must become shorter, deeper and more numerous than in figs. 7 *a*, *b* and *c*; and unless most of these segments become fused in pairs to form diplo-segments, such a degree of shortening would be impracticable and the characteristic pushing power of *Tachypodoiulus* could not be achieved. Thus diplo-segments may have evolved in association with the habit of pushing by means of the legs, and without this fusion of segments in pairs the pushing power of millipedes would be smaller and their burrowing less efficient.

THE NATURE OF THE APPARENTLY SINGLE ANTERIOR SEGMENTS AND THE LOCOMOTION OF THE EARLY INSTARS.

It has been shown above (p. 325) that the possession of only one pair of legs on the anterior rings of millipedes is one of several features which make possible a tight spiral position. These few pairs of legs are also characterized by serving the early locomotory needs of the animal; the body on hatching consists of the head, the legless collum, three leg-bearing segments, two diplo-segments bearing limb buds and the terminal embryonic region, except in the Colobognatha where a second pair of legs is borne by the 4th ring.

Hexapodous running differs from that of many-legged animals in that the instability due to the utilization of less than three supporting legs at any one moment must be avoided, and the greatest stability must be obtained from the few available legs. Fast gaits with backstrokes of shorter duration than the forward stroke

usually cannot be used. If the paired legs are moved in the same phase, either 2, 4 or 6 legs support the body at successive moments, and only two supporting legs give instability except to a jumping animal. But if the paired legs are moved in opposite phase, either 3, 4 or 5 legs support the body at different moments, stability is always maintained, and a more even loading of the legs is also possible.

In bright light, when millipedes tend to seek shelter with all speed, the first instar of *Polydesmus angustus*, 1.16 mm. long, employs a gait of approximately (3.5 : 6.5) with phase differences between successive legs of 0.4 and between paired legs of 0.5 (Pl. 55, fig. 46), a gait commonly found in insects. The animals can momentarily step with the paired legs in similar phase, using the same pattern of gait. This phase relationship between the paired legs contrasts with that of all adult Diplopoda except *Polyxenus* (Part 5), and gives the minimal instability attendant upon the possession of only six legs. The supporting three to five points of the body in the usual gait are well spaced out (Pl. 55, fig. 46), even if less widely spread than in the longer legged insects (see Part 2, text-fig. 3, p. 101). A less stable arrangement would result if the leg-bearing segments were very short, because the legs are short in respect of the growing posterior legless region. The first instar increased in length to 1.5 mm. before the next moult.

The second instar possesses 6 pairs of legs. The pattern of the gait in *P. angustus* is now slightly faster, (5.0 : 5.0) to (4.5 : 5.5), the phase difference between successive legs is reduced to 0.2–0.25; the paired legs usually move in the same phase (Pl. 55, fig. 43), although they can momentarily step in opposite phase, or in any other relationship. The supporting points of the body are evenly spaced, and the disposition of the legs is reminiscent of that of the adult (Pl. 55, fig. 38). As more leg-bearing segments are added, so the phase difference between successive legs becomes reduced in accordance with the principles already discussed (p. 330), making possible the use of more powerful 'lower gears'.

The faster gaits of the second instar and onwards are made possible by the presence of additional legs, which give stability. The gait of the first instar, executed by three pairs of legs, results in 3, 4 and 5 legs pushing for respectively 0.3, 0.5 and 0.2 of the time. If the first instar performed the (5.0 : 5.0) gait of the second instar, the phase difference between successive legs would have to increase to about 0.55*, there would never be more than three supporting legs at any time, and this would mean less stability than is obtained by the (3.5 : 6.5) gait.

Thus it is clear that the employment of a slow gait by the first instar leads to advantageous stability, and that this is aided by the legs being fairly far apart.

In both Diplopoda and anamorphic Chilopoda an increase in leg number after hatching allows the utilization of faster gaits, but in the Diplopoda the advantages resulting from the addition of segments is more significant in respect of additional power than of speed.

Latzel (1884), Silvestri (1903), Attems (1926) and others have supported the view that the anterior 'thoracic' rings of millipedes are single segments, each possessing one pair of legs and tracheal pouches. Silvestri considered that the 'thorax' included the 4th ring. Verhoeff (1901 c, 1910 and 1926), Brölemann (1935) and others have stressed the double nature of the 4th ring, a conclusion supported by the present work, in that functional reasons exist for the loss of a pair of walking legs on this ring in the Eugnatha. Verhoeff, on the other hand, has put forward a reasoned argument in support of the view that rings 2 and 3 also are modified diplo-segments, basing his view upon comparative anatomy of the rings, and on his suggested transformation of the anterior legs of ring 4 into penes and vulva. Pflugfelder's (1932) account of the development of *Playrrhacus*, although not supplying the evidence needed to carry conviction for all his embryological findings, indicates the presence of two coelomic sacs and two ganglia for each thoracic segment.

* The reason for this will be given in a subsequent Part dealing with hexapodous gaits. The increase brings leg 'n+1' on the ground well before leg 'n' is raised.

A preliminary investigation into the development of *Polydesmus* appears to confirm the presence of two ganglionic rudiments on the second to fourth rings.

The second and third rings resemble those behind them in possessing a furrow B, text-figs. 2 and 4 in the Juliformia, Colobognatha, Polydesmoidea and Nematophora, and in its absence from all rings in the Oniscomorpha, corresponding with the furrow Y in Verhoeff's figures (1926). It has been shown above how the presence of this furrow serves similar functional needs on all the leg-bearing rings; it provides a strengthening rib in the Polydesmoidea and in the Nematophora Chordeumoidea for pushing with the 'flat back', it is concerned with forming the non-telescopic inter-ring joints in the Juliformia, Lysiopetaloidae and Colobognatha needed for head-on pushing, and the absence of this furrow in the Oniscomorpha and others is associated with the reduction of the body to a dorsal half cylinder connected with curling up into a 'pill' in which neither of the above features are required. Moreover, the exact form of the furrow in each juliform species is correlated with the shape of the hinder margin of the ring, and thus the furrow does not necessarily mark a junction between two fused segments. It is here suggested that the functional uniformity of the 2nd–3rd and more posterior rings is the basis of their similarity in structure, and that this similarity is therefore flimsy evidence for the double nature of the anterior rings, although the available evidence does suggest that these rings are modified diplo-segments.

If anamorphic development in myriapods is secondary, as has been suggested (see Part 3 and Manton, 1949), the evolution of diplo-segments may have occurred all along the body in an early epimorphic state in association with the habit of pushing. A tendency to assume a spiral position is present in some Onychophora, this habit readily distinguishing *Peripatopsis balfouri* in the field. Such a habit may also have been present in ancestral diplopods. A perfection of the spiral reflex would lead to modifications (referred to on p. 324) of anterior diplo-segments, including a reduction in the number of legs.

The loss of a pair of legs would remove the apophysial function of a pair of tracheal pouches, and the loss of limb musculature would decrease the local respiratory needs. Reference to text-fig. 2 d shows the very small sternite surface available for spiracles and origin of tracheal pouches on the anterior rings, and text-fig. 3 a shows the small space in which two pairs of tracheal pouches are housed in the abdominal region. The acute needs for ventral compression on flexing in the anterior region have already been noted. Ancestral millipedes probably did not have such short rings as shown in text-figs. 2 d and 3 a, but the difficulty of housing tracheal pouches as well as anterior limbs would follow on the perfection of the spiral reflex. The possible disappearance of a pair of tracheal pouches as well as a pair of legs on the anterior rings thus becomes understandable. The development of ganglia in animals tends to follow that of the corresponding mesodermal somites (Manton, 1949). The loss of a pair of legs on an anterior diplo-segment might be expected to be associated with a disappearance in the adult of an external distinction between the two pairs of ganglionic rudiments of the embryo on the anterior rings. There are therefore functional reasons why a few anterior diplo-segments might become modified as seen in present-day Diplopoda, but further evidence is required from embryological work now in progress.

A differentiation of two or three anterior leg-bearing rings from the rest in millipedes clearly has nothing in common with the differentiation of a thorax in insects. It has already been shown how the fusion of segments becomes advantageous when leg-bearing segments are few and the legs long (Part 2, p. 114), resulting in a thorax or prosoma. The leg lengths seen in Part 2, text-fig. 3, p. 101, contrast with those of the young *Polydesmus* shown here on Pl. 55, fig. 46, and the legs of young Juliformia are shorter still. The functional reasons for the evolution of a thorax in other arthropods appear to be quite different from those just considered concerning the anterior trunk segments of millipedes.

MORPHOLOGICAL FEATURES ASSOCIATED WITH LOCOMOTORY HABITS.

Pushing and Rolling Up.

The structural features which appear to be associated with the habits (*a*) of pushing into the substratum and (*b*) of coiling into a defensive spiral when the head and legs are well protected, can now be enumerated.

Common to most millipedes : (1) non-telescopic ball and socket joints (or a derivative thereof) between the rings, the cylindrical form of which allows rotation of one ring upon the next as well as flexure in any plane ; (2) short deep segments, most or all of which are in the form of diplo-segments, and a larger number of legs than is commonly found in other groups of Arthropoda ; (3) strong rigid endo- and exo-skeleton, combining lightness with great strength, and embodying in their construction the principles used in designing steel girders ; (4) trunk musculature capable of rigidly maintaining the flexures between the hard parts at the same time as a propulsive force is exerted by the limbs ; (5) spiracles opening ventrally or ventro-laterally into a space maintained by the stance : (6) provisions allowing acute dorso-ventral flexure along all, or part, of the body, and the tucking under of the head. These provisions include the suppression of anterior limbs and the differentiation of the anterior few rings from the rest ; (7) legs arising mid-ventrally, longer than in primitive Myriapoda and Symphylla, and of the greatest length that can be accommodated without undue lateral projection.

The *Juliformia* show, in addition, features connected with the above and with their speciality of head-on pushing and burrowing into fairly compact earth or mould, etc. : (8) the smooth surface and rounded contours of the body, antennae which lie flat, etc. ; (9) no marked neck on dorsal or lateral surface, broad strong antero-dorsal aspects of head and collum, the latter turning forwards so as to transmit the anteriorly directed thrust of body against a resistance ; (10) the fusion of the component parts of each ring, giving a rigid base for the legs ; (11) the proximal 'head' on the coxa, locked in the ring skeleton, providing the compact extrinsic muscles with a lever for their insertion ; (12) the presence of the furrow B round each ring, which contributes to the formation of non-telescopic inter-ring joints ; (13) the sternite region displaced anteriorly, and with the tracheal pouches so situated as to allow an overlapping of both in acute dorso-ventral flexure, each sternal zone being pulled dorsal to that of the preceding ring ; (14) limited length of the legs, which in the majority do not project much, if at all, beyond the sides of the body ; (15) the large number of short, deep rings, needed to supply sufficient power from relatively short legs ; the most numerous and relatively shorter rings occurring in the larger species.

The *Oniscomorpha* show features which are correlated with head-on pushing and with coiling into a 'pill' additional to 1-6 above : (16) the 'shield', formed by tergite 2 or by tergites 2 and 3 fused, which transmits the forward thrust, and completes the anterior end of the 'pill' ; (17) the small number of rings and the reduction of the body approximately to a half cylinder, with consequent modifications in endo-skeleton and muscles ; (18) flexible pedigerous lamina, five longitudinal hinges between the ventral elements, sternites overlapping from behind forwards, etc. ; (19) the many features which cause the hard parts to fit together neatly, and which also prevent them opening out too far ; (20) a flattening of the limbs in the transverse plane, the wide bases of the coxae and the form of the limb flexures ; (21) the locomotory force originating in the limb muscles being supplemented by muscles which move the tracheal pouches antero-posteriorly.

The *Nematophora* (Chordeumoidea) show features additional to 1-6 and 21 which appears to be correlated with pushing by the dorsal surface and with running more speedily than other millipedes : (22) longer legs which hinder burrowing in compact material, but provide increased power and speed, and the presence of a trochanter (see p. 362) separate from the coxa ; (23) projecting keels (*Polymicrodon* and *Craspedosoma*) which increase the pushing surface and give some protection to the legs ;

(24) dorsal median groove and curved buttresses on the skeleton providing strength, the transverse groove B providing a strengthening rib between the limbs and dorsal surface ; (25) sternites which can increase their overlap from before backwards, a median papilla stopping each sternite from pressing too closely on the limbs of the following sternite ; (26) extrinsic muscles from the coxa crossing to the opposite side of the body, and bracing the base of the leg against the thrust which can be exerted by the dorsal surface, and a 'head' on the coxa in principle resembling (11) that of the Juliformia (text-fig. 8 b) ; (27) a more mobile neck and a small collum ; (28) the presence of about 30 rings may be correlated with legs longer than in Juliformia and Oniscomorpha and the presence of keels (see p. 360).

The *Polydesmoidea*, such as *Polydesmus*, are the most powerful of the millipedes here examined ; they are adept at forcing a way into cracks but cannot burrow in compact soil owing to the length of the legs and presence of keels. They show, in addition to features 1-6, 10 and 22 : (23) keels almost as in the Nematophora Chordeumoidea, but more strongly developed, and with dorsal sculpturing instead of a dorsal groove ; larger keels necessitate (29) longer and fewer rings than in the Chordeumoidea (see also p. 359) ; (26) in principle as in Nematophora, but differing in details ; (30) longer legs which are stouter than in other millipedes, particularly in males ; (31) ventral dilatations of the rigid pedigerous lamina, which house long and short extrinsic leg muscles and allow (32) a lateral origin of the limbs and laterally directed spiracles.

The *Colobognatha*, exemplified by *Polyzonium*, combine the several specialities of the former orders, but each capability is less advanced. *Polyzonium* is not fleet, but is not as slow as the Oniscomorpha ; it pushes mainly by the head end, but the dorsal surface takes the resistance, and it is a moderate burrower. Features (1) and (3) are less effectively developed, (2), (4) and (21) are present ; (6) has not involved the anterior legs on ring 4 because the head is small. The pedigerous lamina and sternites are intermediate between (18) and (25), the sternites are median as in Nematophora, but when the body is straight they do not overlap.

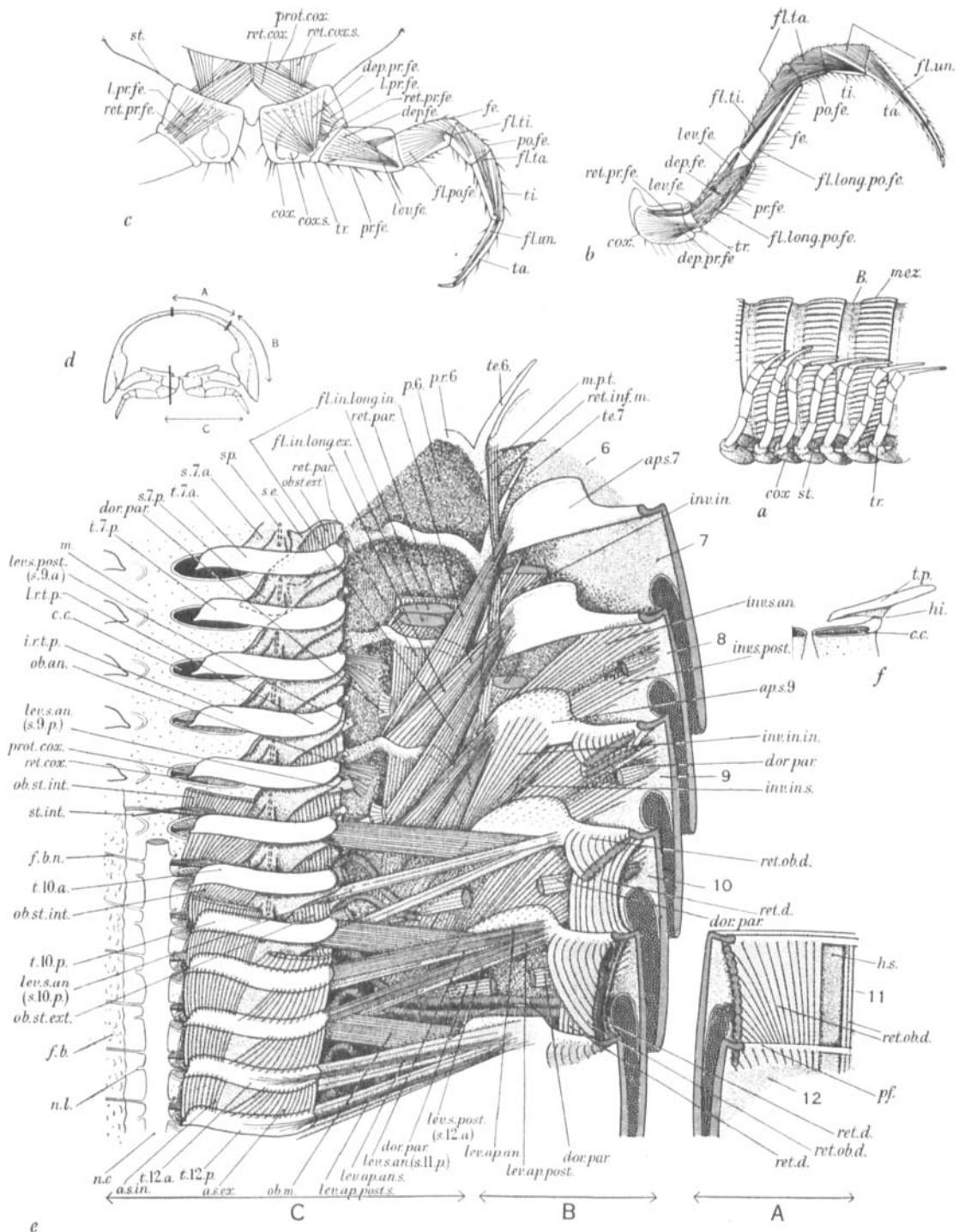
The changeable shape of the body combines to some extent the advantages of a cylindrical ring (Juliformia, etc.), with one approximating to a half cylinder (Oniscomorpha), and the projecting junction of tergite and pleurite to some extent gives the same advantage as the keels of Polydesmoidea and Nematophora.

This long list of features associated with pushing into the substratum and with curling up embraces the more conspicuous features of millipede morphology, excluding the head, feeding and sense organs, gonopods and viscera, and therefore indicates the importance of the part played by these habits in the evolution of the group.

There are other accomplishments correlated with structure which are less widespread in their occurrence and concern certain groups only.

Rock-climbing.

A marked ability to climb on smooth rock surfaces at any angle is found in *Polyzonium* and among the Nematophora in the Lysiopetaloidae, which are also fitted for pushing in stony places (p. 361). This climbing habit necessitates a powerful grip by the legs of a pair, and possibly the use of adhesive coxal sacs when the animal rests. In summer *Polyzonium* walks upside down across smooth chalk boulders, where it may remain for hours or days hanging on in a chiton-like manner, with neither head, antennae nor legs exposed. The coxae are held close to the rock, and the body is flattened (text-fig. 4 h), so that the keel-like lateral angles cover the legs closely and approach much nearer to the substratum than in text-fig. 4 g, a compensatory elongation of the body making so great a change in shape possible. Sensory spines on the coxa and prefemur of the length shown in text-fig. 8 c must be of importance. During the winter *Polyzonium* penetrates into compact vegetable matter and leaf mould, frequently deep in moss, where it remains curled up for weeks without moving, and is difficult to find in spite of its



TEXT- FIG. 8.

a and **b**: *Lysiopetalum illyricum*, (a) lateral view of a few rings showing the 'furled' position of the legs; (b) single leg showing the segments and muscles; (c) *Polyzonium germanicum*, posterior view of legs and sternite; (d and e) *Sphaerotherium giganteum*, the diagram (d) shows the normal positions of the sections of the body A, B and C which are opened out in (e) where

bright orange colour. No other available millipede has been found capable of walking and remaining upside down on a fairly smooth glass surface, but the Lysiopetaloidae may be expected to be able to do this also. The Juliformia walk upside down on a rock surface ineffectively; some species readily fall off, others cannot do it at all. The Oniscomorpha cannot walk upside down; the Polydesmoidea can hold on to wood and bark in any position, although they do not normally choose to hang upside down for long; *Microchordeuma* readily runs over the underside of a stone but *Polymicrodon* falls off more easily.

The limb musculature of millipedes controls the types of leg movements which can take place, and thus the gripping or pushing abilities. Four extrinsic muscles are found only in the Polydesmoidea and Nematophora, the longus muscles crossing to the opposite side, in contrast to the two coxal muscles present in other orders. The four coxal muscles allow the animals to push with the dorsal surface (p. 313). The retractor coxae of the Colobognatha must function in a similar manner, it partly

LEGEND TO TEXT-FIG. 8 (*continued*).

the dorsal body wall A is cut off, the lateral body wall B is turned outwards away from the ventral section C, the viscera, fat body and most of the tracheae are removed to display the musculature and endoskeleton, the dissection being carried progressively deeper towards the anterior end of the section of the body shown; (f) posterior view of the union between the coxa and tracheal pouch.

For key to lettering on figs. a-c see legend to text-fig. 3, p. 309.

<i>a.s.ex.</i>	musculus apophysis sternalis externus.	<i>m.</i>	flexible membrane between sclerites and leg bases.
<i>a.s.in.</i>	musculus apophysis sternalis internus.	<i>m.p.t.</i>	flexible membrane forming hinge between pleurite and tergite.
<i>ap.s.7, ap.s.9.</i>	apophysis squamosi lateralis of the 7th and 9th rings respectively.	<i>n.c.</i>	nerve cord.
<i>c.c.</i>	internal cavity of coxa.	<i>n.l.</i>	nerve to limb.
<i>dor.par.</i>	dorso-paratergalis.	<i>ob.av.</i>	obliquus anticus, anterior part, the posterior part is not labelled.
<i>f.b.</i>	fat body.	<i>ob.m.</i>	obliquus medius.
<i>f.b.n.</i>	nerve to fat body.	<i>ob.st.ext.</i>	obliquus sternalis externus.
<i>fl.in.long.in.</i>	flexor inferus longus internus.	<i>ob.st.int.</i>	obliquus sternalis internus.
<i>fl.in.long.ex.</i>	flexor inferus longus externus.	<i>p.6.</i>	pleurite of 6th ring.
<i>h.s.</i>	dorsal gap in musculature occupied by heart.	<i>p.r.6.</i>	upturned anterior edge of pleurite of 6th ring.
<i>hi.</i>	hinge between coxa and strut from tracheal pouch.	<i>pf.</i>	prophragma.
<i>i.r.t.p.</i>	inner ramus of tracheal pouch.	<i>prot.cox.</i>	protractor coxae.
<i>inv.in.</i>	involvens inferus cut down to expose tendon (white) from the following ring.	<i>ret.cox.</i>	retractor coxae.
<i>inv.in.in.</i>	pars infera involventis inferi.	<i>ret.d.</i>	retractor dorsalis.
<i>inv.in.s.</i>	pars supra involventis inferi.	<i>ret.inf.m.</i>	retractor inferus mesotergiti.
<i>inv.s.an.</i>	pars antica involventis superi.	<i>ret.ob.d.</i>	retractor obliquus dorsalis.
<i>inv.s.post.</i>	pars postica involventis superi.	<i>ret.par.</i>	retractor paratergalis.
<i>l.r.t.p.</i>	lateral ramus of tracheal pouch.	<i>s.e.</i>	anterior back-curved edge of sternite.
<i>lev.ap.an.</i>	levator apophysis anticae.	<i>s.7.a.</i>	anterior sternite of 7th ring.
<i>lev.ap.an.s.</i>	pars superficialis levatoris apophysis anticae.	<i>s.7.p.</i>	posterior sternite of 7th ring.
<i>lev.ap.post.</i>	levator apophysis posticæ.	<i>sp.</i>	position of spiracle on ventral side.
<i>lev.ap.post.s.</i>	pars superficialis levatoris apophysis posticæ.	<i>st.int.</i>	sternalis intersecatus.
<i>lev.s.an.(s.9.p.), lev.s.an.(s.10.p), lev.s.an.(s.11.p)</i>	levator sternalis anticae to the posterior sternite of rings 9, 10 and 11 respectively.	<i>t.p.</i>	tracheal pouch.
<i>lev.s.post.(s.9.a), lev.s.post.(s.12.a),</i>	levator sternalis posticæ to the anterior sternite of rings 9 and 12 respectively.	<i>t.7.a., t.10.a., t.12.a.</i>	anterior tracheal pouch of 7th, 10th and 12th rings respectively.
		<i>t.7.p., t.10.p., t.12.p.</i>	posterior tracheal pouch of 7th, 10th and 12th rings respectively.
		<i>te.6., te.7.</i>	tendon from 6th and 7th rings respectively.
		<i>6-12.</i>	tergites of 6th to 12th rings respectively.

crosses over in *Pseudodesmus* (Silvestri, 1903, fig. 326), and in *Polyzonium* the pair meet in the middle line (text-fig. 8 c). Both the retractor and protractor coxae of *Polyzonium* run inwards towards the middle line in contrast to their positions in the Juliformia where the gripping ability is less (compare text-figs. 3 c and 8 c).

The legs of *Polyzonium* are shorter than in most millipedes (Table I), and they are wide in the transverse plane, particularly at the base, as in the Oniscomorpha. A longer leg would not be covered by the sides of the body. The coxa houses four muscles moving the prefemur in the Opisthandria (see Silvestri, 1904, fig. 331) and three in *Polyzonium* (text-fig. 8 c), while other millipedes possess but two such muscles (see text-figs. 3 c and f). The powerful grip exerted by each pair of legs in *Polyzonium* must be due to the wide coxa, allowing a large depressor prefemoris, to the more proximal spread of the flexores tibiae, tarsi and unguiculi than in the Juliformia and Polydesmoidea, a feature also seen in *Lysiopetalum* (see p. 361 and text-figs. 2 g, 3 c, and 8 b and c) and to the distal joints between the segments of the limb being hinged on the dorsal side (text-fig. 8 c), as in most millipedes.

Text-fig. 8 c shows the large ventral shoulder on the coxa of *Polyzonium* housing the coxal sac, an eversible organ apparently evaginated by blood pressure and provided with large retractor muscles. The function of coxal sacs is uncertain. They occur on most legs of both sexes of millipedes only in the Colobognatha and Lysiopetaloidea, these being two groups with rock climbing abilities; the large size of the retractor muscles suggests that the coxal sacs might be used for adhesion, assisting the legs during prolonged hanging from the underside of rock surfaces. An adhesive function has been suggested for the protrusible vesicles of the ventral tube of Collembola (Imms, 1942). Tiegs (1949) has shown that water absorption is a function of the coxal sacs in Symphyla, and a similar suggestion has been made for these organs in the Diplura and Thysanura (Imms, 1942). The coxal sacs of the Colobognatha and Lysiopetaloidea also may be used for absorbing moisture. The presence of coxal sacs in these groups has been regarded as a primitive feature (Verhoeff, 1901 b), but the suggestion that they represent the 'reins coaux' or 'segmental organs' of the Onychophora (Brölemann, 1935; Wood-Mason, 1879) has little to commend it. Coxal sacs of the Arthropoda *vera* have more in common with the coxal organs, which are found in some onychophoran genera such as *Peripatus* and *Opisthopatus* (Purcell, 1900) whose function is unknown, than with the segmental excretory organs or 'nephridia' which are present in all Onychophora.

THE EVOLUTION OF THE DIPLOPODA.

Primitive and Specialized Features, the Colobognatha and Oniscomorpha.

The range of gaits shown by all groups of Diplopoda is remarkably wide compared with other many-legged arthropods (see Part 2, p. 105, Table 2), but no one order can be regarded as showing a primitive myriapodan condition. The Diplopoda as a whole are highly specialized, both in the locomotory mechanisms and in their associated morphology. It has been shown why a large number of legs is essential for the employment of powerful 'low gears' (p. 330) and how the many-legged state has been made practicable (pp. 346 and 304-324). Attems (1926) noted the reasons why no existing group of millipedes can be regarded as having had the potentiality of giving rise to all the others.

Many of the most primitive animals living today appear to have remained so because they have also become highly specialized in some limited way. The Monotremata are a well-known example, and *Polygordius* may be another in which it has been suggested (Manton, 1949) that the persistence of a primitive manner of development of the whole trunk region may be due to the great elaboration of the prototroch. The Colobognatha may be a further example. Apart from characters 1-7 on p. 352, the greatest specializations of *Polyzonium*, the only available representative of the group, concern rock climbing, which affects the body and legs (p. 353), and an unknown

manner of feeding affecting the head and mouth parts. Except for rock climbing, the range of capabilities of the Colobognatha clearly represents a more primitive level than is found in the other orders, which show restricted but perfected activities. The chiton-like habit of *Polyzonium*, made possible by leg structure, changeable shape, and possibly by the coxal sacs, may be a general accomplishment within the Colobognatha.

Systematists have recognized a greater number of primitive features in the Colobognatha than in the other orders, features such as the primitive condition of the 4th ring, the more leg-like form of the gonopods and the state of the inter-ring joint (see also p. 323). Verhoeff (1926, pls. 6 and 7) regards free pleurites also as primitive, since Permian diplopods show this feature. However, these fossils appear to be more advanced than the Colobognatha in their longer legs.

If free pleurites characterized primitive millipedes, presumably free sternites were also present, but it is unlikely that a locomotory force, implemented by sliding the tracheal pouches backwards and forwards, was a primitive character. Peripatus does not shift its leg bases. The range of movement of the sternites of *Polyzonium* appears to be smaller than are those of the Oniscomorpha and Nematophora, and the form of the sternites of *Polyzonium* is more primitive than in the other two orders in that the sternites do not overlap when the body is straight, and butt up rather than overlap on dorso-ventral flexure. The overlap of the nematophoran sternites from before backwards and of the laterally placed oniscomorphan sternites from behind forwards are mutually exclusive. Both could have been derived from a primitive stock in which neither antero-posterior sliding nor overlap of the rigid parts of the sternites took place. Such sternites were probably short, packing together much as in *Polyzonium* on flexure, and from such a condition that of the Colobognatha, Nematophora and Oniscomorpha could have been derived. A convergent evolution of larger apophyses from the tracheal pouches, and more elaborate muscles to move them and the limb bases backwards and forwards, must have occurred independently in the Oniscomorpha and Nematophora; and the inter-tracheal pouch musculature of either could have been derived from the simple pair of longitudinal muscles uniting the tracheal pouches and sternites of *Polyzonium* (see Verhoeff, 1928, fig. 728), together with the entirely different methods of overlapping of the sclerites (see also Appendix).

There is no direct indication as to the stage at which a median sternite was evolved. No functional advantage can be suggested for the existence of paired sternites in a primitive millipede already possessing the pushing and burrowing habit and mid-ventral origin of its limbs. A median sternite would appear to be the more advantageous, except in animals specializing in (1) rolling up and (2) doing so by reduction of segment numbers, and (3) maintaining power by thickening the remaining legs, which leads to very little or no space being available for hard parts mid-ventrally around the leg bases, as in the Oniscomorpha. The fusion of the sternites with the rest of the ring in the Juliformia, Polydesmoidea, and in a few Colobognatha gives rigidity to the limb base by means of the skeleton, and an abandonment of the primitive use of muscles for this purpose, as seen in the Onychophora, and as occurred presumably in Archi-diplopoda.

It is suggested below that the presence of a well-formed trochanter on the leg between the coxa and prefemur in the Lysiopetaloidae (text-fig. 8 b, *tr*) is correlated with the marked ability to curl the leg up over the ventral edge of the tergite. This segment, which always lacks muscles of its own, is small but distinct in other Nematophora (text-fig. 2 o and p), and probably serves the same purpose. In the Polydesmoidea and Juliformia the trochanter is not separate from the coxa (text-fig. 3 d and f), the base of the leg thereby possessing stability and a desirable limitation in its movements (p. 314). It is possible that the presence of a movable trochanter may have been a primitive feature possessed by millipedes at a stage when they all possessed free sternites; that the segment has persisted in the Nematophora where the long legs fold up against the body; and that it has become

fused to the coxa in the Polydesmoidea and Juliformia where fusion of the sternites with the tergite removes any projecting ridge, and therefore any need for this joint. The flatness of the ventral side of the Oniscomorpha and of *Polyzonium*, together with the shortness of the leg in the latter, also removes the need for the trochanter, although free sternites are present. The short wide trochanter of *Polyzonium* probably does not confer added mobility to the leg.

Two theories have been put forward to account for the numbers of body segments in different animals, both for millipedes and centipedes, and either long or short bodied forms having been considered primitive. For millipedes as for centipedes (Part 3) functional reasons can be suggested for adopting a middle course, rather than the 'Elongationsprincip' of Verhoeff (1901 a) or the 'Kondensationsprincip' of Nemec (1901), Attems (1926) and Brölemann (1921). Lawrence (1952) has pointed out that Arthropods with small numbers of body segments tend to show fixed numbers either within the species or the group. The belief that an indefinite number of segments is more primitive than a fixed number favours a suggested primitiveness of the Juliformia and Lysioptaloidea which possess a variable, but large number of rings, and the clear secondary reduction in segment numbers within the Opisthandria indicates that the smaller numbers are here the more specialized. *Glomeridesmus* (Limacomorpha) possesses 20 rings and curls into a moderate 'pill' (Pl. 54, fig. 35), although Attems (1926) states the contrary for the Limacomorpha: "Körper nicht in ein Kugel einrollbar". Progressive specialization for rolling up has probably led to the more perfect 'pills' seen in the Oniscomorpha, *Sphaerotherium* with 21 pairs of legs and a shield formed only by the 2nd ring being more primitive than *Glomeris* with 17 pairs of legs and the 3rd tergite fused with the second. (This does not imply that the Oniscomorpha have ever possessed anterior tergites as seen in the Limacomorpha.)

It has been assumed that a similar shortening has occurred in the Nematophora and Polydesmoidea. In the former the Lysioptaloidea possess over 40 rings, and the Chordeumoidea fixed numbers of 26-32 rings, most species showing 30. In the Polydesmoidea the range is 19-28 rings, the majority of species possessing 20. The smaller numbers in each order have been considered to be the least primitive. Attems (1926) noted that there is no obvious reason for the supposed reduction in ring numbers in the Nematophora and Polydesmoidea, although he believed it to have taken place. It is suggested below that the large number of rings in the Lysioptaloidea is not primitive.

Primitive Millipedes.

It has been shown above how a shortening and deepening of the body segments and an increase in their number must have increased the pushing power of an ancestral millipede and led to the formation of diplo-segments and ball and socket joints, so rare outside chordates and echinoderms (p. 348). The acquisition of the mid-ventral origin of the legs would appear to have originated in conjunction with the burrowing habit of such an ancestor. Mechanical difficulties must have been encountered, particularly in effecting a close dorso-ventral flexure. Beyond the stage at which the pushing habit had led to the formation of diplo-segments, the paths of the several orders appear to have diverged, primarily in association with the finer details of their habits.

The same problems have been solved in different ways by the several orders, and parallel evolutions of the same solutions have occurred. Examples are seen in the various methods of rolling up (p. 324) in the 'pill' millipedes of various groups (p. 321) and in the several occurrences of keels (p. 327). The development of four extrinsic coxal muscles, the longus pairs crossing to the opposite side of the body and differing in details in the Polydesmoidea and Nematophora, must have evolved independently along with the long powerful legs and particular pushing habits. The narrow coxal articulation with the ring in the Nematophora and Juliformia

(text-figs. 3 d and 8 b) is a parallel evolution associated with the cylindrical form of the body. The unconstricted base of the coxa in the Polydesmoidea is correlated with the laterally directed limb origin. The wide coxal articulations in the Oniscomorpha and in *Polyzonium* are associated with the flatter ventral surfaces. The various functions performed by the constriction B in the several orders are referred to on pp. 305, 351, etc. Further examples of parallel evolution have been noted in the account of the muscular systems.

Juliformia.

Burrowing by the head end is suggested as a habit of predominant importance in the evolution of the Juliformia, the burrowing being carried well below the litter of woodlands to which the longer legged Polydesmoidea and Nematophora are largely restricted. Leg length is limited by the habit (p. 342) and the evolution of many short deep rings has been shown to be associated with the provision of adequate pushing power (p. 346). Efficient burrowing is only possible within a certain size range (pp. 345 and 348). Progressive elongation of the body, in the sense of adding more rings but maintaining the same overall shape, represents evolutionary progress in the Juliformia. The acceptance of the latter conclusion does not imply that the shortest existing millipedes in all other groups are the most primitive. We can only guess the number of rings possessed by the ancestral stock at the time when diplo-segments were evolved and before the modern orders diverged. It is suggested here that the larger Juliformia with the more numerous shorter rings represent the culmination of a line of evolution which cannot be advanced further for mechanical reasons, and that such millipedes cannot be considered primitive (p. 346). Indeed, many of the larger species of Spirostreptomorpha, whose size renders them poor burrowers, have taken to a more exposed way of life, and travel considerable distances. The long legs of *Plusioporus* (Table I and Pl. 53, fig. 24) may be associated with such a habit.

The acquisition of longer legs gives increased speed and power, but limits the type of substratum which can be penetrated. It is possible that an early development of longer legs and a habit of pushing by the dorsal surface rather than by the head end took place in the ancestors of the Nematophora Chordeumoidea and of the Polydesmoidea before the tendency to shorten and deepen the rings and increase their number had been carried very far, and it is unlikely that these groups ever possessed as many rings as can be found in the Juliformia. There appears to be no direct evidence as to whether the species in each order possessing the greater or the smaller number of rings are the more primitive, although analogy with the Oniscomorpha and other arthropodan groups has inclined opinion towards regarding the smaller numbers as the more specialized.

Polydesmoidea.

The evolution of the Polydesmoidea appears to have been associated with the habit of pushing by the 'flat back' into the layered decaying leaves of a woodland floor and other matter which tends to split open along one plane, rather than into the soil. Pushing by the dorsal surface uses a greater area for the application of the force than pushing by the head end as in the Juliformia, and the force appropriate for pushing by the dorsal surface is greater. The Polydesmoidea possess the most powerful legs and most fully developed keels to be found among millipedes. A large keel will contribute most to enlarging the dorsal surface and to giving cover for the leg, but it cannot be borne on a short ring because lateral bending of the body would be impaired (p. 313). Whether the rings of the Polydesmoidea have undergone secondary elongation and a reversal of the primitive tendency to become shorter has yet to be proved. The diplo-segments of *Polydesmus* are

relatively shorter than are two segments of any centipede or of Peripatus walking moderately fast (Table I) and they represent some 40 single segments, a number larger than those of most Onychophora and the more primitive number envisaged for the Chilopoda (see Part 3). Thus a shortening of the segments appears to have taken place to some extent in the Polydesmoidea, and if the characteristic habits of these animals were established early, the group may never have progressed as far as other millipedes in shortening the rings and adding to their number. On the other hand, it is perhaps more probable that the evolution of longer, stouter legs and larger keels occurred long after the acquisition of diplo-segments. The evolution of keels above a certain size must necessitate a secondary elongation of the rings and a reduction in their number if the flexibility of the body and the usual overall shape is to be maintained. This number of rings will be expected to be smaller than in the Nematophora Chordeumoidea (see below).

Nematophora.

The problems of life in woodland litter have been solved by the Nematophora in a different way, giving a remarkable convergence to the Polydesmoidea in the habit of pushing with the dorsal surface (pp. 326, 341 and 343), and with this is associated fairly long legs, extrinsic limb muscles which cross over, and in the Chordeumoidea the frequent appearance of keels. The Nematophora have achieved extra power by exploiting the possibilities of the primitively free sternites in a manner parallel to that of the Oniscomorpha, and their fleetness may be correlated with the adoption of a more omnivorous or carnivorous diet (see below).

The presence of more rings in the Nematophora than in the Polydesmoidea, and the smaller size of the nematophoran keels are probably both associated with the presence of free sternites. It has been shown how Juliformia of very different sizes but similar habits exert the same order of pushing force per unit of transverse sectional body area (p. 348). Litter living Polydesmoidea and *Polymicrodon* might need comparable pushing powers if their habits were identical. The pushing power which can be exerted by a ring of *Polydesmus* is greater than that exerted by an equal sized ring of *Polymicrodon* or *Craspedosoma* (see Table I, column 1 and left side of column 8), but the total pushing powers of these animals (column 9) are less unlike because of their different number of body rings (the entries in column 9 are of no real significance in the life of the animals but are given because of the difficulty of estimating the area of the dorsal pushing surface of a 'flat backed' millipede). In *Polydesmus* much of the musculature directly contributes to dorsal pushing, since rigid skeleton holds the base of the leg. In the Nematophora, however, part of the musculature prevents the legs from displacing the free sternites upwards, and thus energy is used to oppose the leg muscles in dorsal pushing. To attain comparable power the Nematophora would be expected to possess more rings than the Polydesmoidea, and if the same overall shape is maintained, the rings must be shorter and keels, if any, smaller. Actually many Nematophora are relatively longer than other millipedes (p. 345), perhaps indicating that the need for power is greater than the advantages conferred by the average overall shape, and even with the longer body *Polymicrodon* is less powerful than *Polydesmus*. If the characteristic litter living habits were adopted when the ancestral stock had acquired no more than about 30 rings, the modern Chordeumoidea may never have possessed a greater number, and there appears to be a functional explanation for this number being larger than in the Polydesmoidea.

The presence of keels, which assist in pushing by the dorsal surface and in providing cover for the legs, is a hindrance in head-on burrowing. A tendency to find cover for the legs, whether well formed keels are present or not, may have led to the separation of the trochanter from the coxa in the Nematophora which allow the legs to furl close against the sides of the body over the ventral edges of the tergites, a tendency which appears to have contributed to the burrowing and other special abilities of the Lysioptaloidea.

The nematophoran suborder Lysiopetaloidea occupies a position of interest. Attems (1926) called attention to the absence of sharp dividing lines between the Juliformia, Nematophora and Polydesmoidea, and to the resemblances of the Lysiopetaloidea to all three groups. The Lysiopetaloidea lack keels and are heavily armoured. The legs and antennae are long and the sternites free. The tergites are shorter than in the Chordeumoidea, more juliform-like in shape and over 40 in number. In *Lysiopetalum illyricum* the (leg length/ $\sqrt[3]{}$ ring volume) is 2·0 and the (depth/length) of a ring is 4·0 (compare with other entries in Table I). The appendages of the 7th ring resemble those of the Polydesmoidea. The collum is larger than in *Craspedosoma* but does not form such an effective ramming point as in the Juliformia.

Unfortunately no living representative of the Lysiopetaloidea has been available. This group is restricted to the Mediterranean and Balkan regions, and occurs in stony places devoid of vegetation, under large rocks, and in caves. Verhoeff (1926) notes that these millipedes live in such a manner that they must go and seek their food, instead of being surrounded by it, as is the case with the majority of millipedes. Verfasser (1900), quoted by Verhoeff (1926), found *Apfelbeckia landenfeldi* on the walls of completely bare caves. He kept them for a considerable period and they refused all vegetable food, but took dead flies, geophilomorpha, living earthworms and a phalangid, eating the whole of the prey. The Chordeumoidea are fleet than any other millipedes recorded above, and they are omnivorous, insect remains as well as plant material being found in the gut. The Lysiopetaloidea appear to have gone a stage further in adopting a carnivorous diet, and presumably the marked unpleasantness of the discharge from their stink glands, the contents of which pours out more rapidly than in other millipedes, together with the evil smelling fluid squirted from the rectum (Verhoeff, 1926), is associated with the aggressive tendencies and more exposed habits of this group.

Löhner's (1914) photographs of *Lysiopetalum illyricum* show the same type of limb movement as seen in the Chordeumoidea (Pls. 53, 54, figs. 18, 20, 28). Gait (6·7 : 3·3) is shown by Löhner's pl. 10, fig. 21 of 'very fast running'. It is probable that this millipede is indeed a very fast runner, because a gait as fast as this has only once been recorded in the present work. The carnivorous diet, and a need to go and search for food, would make fast moving more desirable to this group than to all others. Löhner's photographs of 'slow walking', figs. 17 and 18, indicate gaits of about (4·8 : 5·2) and (5·0 : 5·0), showing that the animal was then still using moderately fast gaits. It can thus be concluded that *Lysiopetalum* is probably a fleet carnivore.

The Lysiopetaloidea are unique among millipedes in several respects. The legs in running are held as in *Polymericodon* (Pl. 53, fig. 18), but owing to their structure they can grip a rough surface very firmly and can furl very closely up and against the sides of the body (text-fig. 8 a), and in this position the leg tips can be powerfully flexed downwards, backwards and outwards. The leg is curved and cannot lie in any one plane. The trochanter (text-figs. 8 a and b) enables the leg to curl up and over the ventral edge of the tergite, and the retractor prefemoris and levator femoris hold the leg close in. The long tarsus is partially divided in this group alone, and the distal part of the tibia is wide. The leg is clothed with spines which are particularly long on the ventral side. The musculature of the whole leg is adapted to give a particularly powerful distal flexure. In *Polydesmus* a very regular series of flexor muscles is present all along the leg (text-fig. 2 g). In *Lysiopetalum* the flexor unguiculi arises from the whole length of the tibia instead of from its distal half. The flexor tarsi is larger than in any other described group of millipedes, arising from nearly the whole length of the femur and postfemur. The flexor tibiae arises only from the proximal end of the prefemur, and directly pulls against the strap-like levator femoris. The flexor muscle to the postfemur is also strap-like, very long and ventral in position, extending through the whole of the femur and prefemur, *fl.long.po.fe.* The long narrow levator femoris, flexor tibiae and flexor longus

postfemoris above and below, and the very large fan-shaped flexores tarsi and pretarsi must give great power to the tip of the leg. No other group of millipedes shows such leg structure. The Juliformia cannot hold their legs in this position, even when the legs are fairly long.

Polymericodon and *Craspedosoma* have smaller trochanters, and strap-like levator femoris and flexor longus postfemoris muscles are present, but the leg tapers, and flexores tibiae, tarsi, and unguiculi form an even series. The occurrence of coxal sacs and sensory spines projecting ventrally from the basal segments of the leg of *Lysiopetalum* and *Polyzonium* (text-figs. 8 b and c), in contrast to the paucity of spines in this position in millipedes which do not rock-climb (text-figs. 3 c and f and 4 d), is probably significant.

The leg structure of the Lysiopetaloidea and the many short trunk rings must provide great power per unit of transverse sectional area of the body, and suggests that these animals are expert rock climbers and negotiators of crevices, and that they are powerful burrowers, probably in stony places, besides being fast runners. Legs with a particularly strong distal grip, with the ability to work in a 'furled' position close to the sides of the body, which possess mobile tips which can grip outwards and backwards, and an array of powerful spines all along the leg, must equip the Lysiopetaloidea more suitably for such a habit than any other millipedes, where the legs grip mainly in a downward direction. The very stout ridges on the metazonite of *Lysiopetalum* (text-fig. 8 a) and the less pronounced ones on *Callipus* may also provide a grip when needed, besides strength to resist rough surfaces. Burrowing could also be pursued by the same technique. The short rings bring the legs close together, their spines spanning the gaps between them; one leg gives cover for the next, and none need project far from the body. A ventral air space can no longer be maintained in this stance, but the very deep coxae, continually shifting forwards and backwards, must maintain free access of air to the spiracles during burrowing. The crossed longus muscles to the coxae suggest that pushing by the dorsal surface is still practised, and the larger collum and more numerous rings giving added power suggest a marked ability to push forwards.

Thus a habit initially resembling those of the Polydesmoidea and Chordeumoidea may have been succeeded by particular development of fleetness for catching live prey, a strong grip for walking on rock surfaces, and the ability of pushing by the legs in a 'furled' position when needed in stony places, rather than by using the outstretched tip as in the Juliformia. The shortness of the rings and an increase in their number appear to be convergent similarities to the Juliformia, and may have been acquired in association with similar functional needs, and cannot be regarded as primitive nematophoran features.

Conclusions.

Thus functional considerations suggest that a moderate number of rings may have characterized an archi-diplopod, its diplo-segments having increased the pushing ability; that differentiation of habit, either for a continuance of pushing by the head end or for pushing by the dorsal surface, is correlated with segment numbers, the larger numbers having been acquired in a parallel manner by the Juliformia, Lysiopetaloidea and Colobognatha in association with the former habit, moderate numbers having been either maintained or obtained by reduction in the Chordeumoidea and Polydesmoidea and a secondary reduction to smaller numbers occurring in the Oniscomorpha. The implication that the Lysiopetaloidea first pursued a habit in common with the Chordeumoidea and later changed to one partly resembling that of the Juliformia is not unreasonable. The geophilomorph centipedes must have first evolved much as did the Scolopendropmorphs, both groups perfecting their gaits and morphology in association with increase of speed and running round obstacles, and only later must the geophilomorpha have abandoned the pursuit of speed in favour of an entirely different habit, that of burrowing by using the body muscles and not the legs.

Brölemann (1931 and 1935) has favoured a different grouping of the larger divisions of the Diplopoda to that used by Attems and adopted here, and links the Spirostreptomorpha with the Polydesmoidea, considering the Polydesmoidea to be abbreviated derivatives of the Spirostreptomorpha. The present work does not support this view. The fundamental differences in habits of the two groups are correlated with very different structure, differences in the form of the ring, skeleton, muscles and limbs, and these appear far to outweigh the claimed similarities. The Spirostreptomorpha comprise many of the largest and most successful of the Juliformia, possessing the most numerous, short, deep rings, which are here considered to be the highest specialization, and there are no known examples of juliform millipedes which appear to have taken to a mode of life so different that their evolutionary changes have been reversed.

Power for pushing or for fast running is dependent upon advancements in leg structure, but within a group it has been shown how the design of the body for speed and power is a compromise (Juliformia, p. 342). Similar examples can be found in vertebrates and other animals. Speed has been attempted several times by millipedes, litter living species are fleet than burrowers. Some of the larger Juliformia move about rapidly by longish legs, such as *Plusioporus*, but speed is more marked in the Nematophora, and has doubtless made possible the carnivorous habits of the Lysiopetaloidae. In both the Nematophora and Polydesmoidea the legs are relatively longer than those of the scolopendromorph and lithobiomorph centipedes (Table I, column 4), the short wide rings and limb origin of the millipedes masking the considerable length of their legs.

The Polydesmoidea are conspicuously powerful and fairly fleet, but one member may have acquired speed in a most spectacular manner. *Pandirodesmus disparipes* (Silvestri, 1932) from Guiana has elongated its legs to a degree approaching that of the scutigeromorph centipedes, the (leg length/ $\sqrt[3]{\text{ring volume}}$) is 3.7, while the corresponding figure for *Scutigera* (leg length/ $\sqrt[3]{\text{volume of 2 segments}}$) is 5.6 (see entries on Table I, column 4). The difficulties attendant upon elongation of the legs of a many-legged animal when the fields of movement of successive legs overlap greatly have been noted in Part 2, p. 99. A unique solution of the problem is shown by *Pandirodesmus* in which alternate legs are long and short, the longer pair arising from the body slightly above the shorter pair, and presumably the shorter legs step under the arch formed by the longer ones. The tarsus is also provided with long gripping spines, a feature also found in the longest legged centipedes (Part 3). It is probably significant that such a long legged millipede occurs in the Polydesmoidea, a group already possessing fairly long legs and in which the ring supplies a rigid base for their operation. No order possessing free sternites would be expected to be able to carry so long a leg. However, the rarity of the *Pandirodesmus* condition does not suggest that the double row of legs has been a very great success. The habits of *Pandirodesmus* have not been recorded, but the absence of eyes as in other Polydesmoidea, suggests a continuance of a vegetarian diet.

Reference has been made above to a limited number of millipedes, and it is clear that within each group there are considerable differences in detailed habits of life. Nevertheless the animals which have been examined represent the major divisions of the Diplopoda, and indicate what are believed to be the salient features of the locomotory mechanisms and associated morphology. The Diplopoda as a whole show great specialization, centring on the production of power from 'bottom gear' gaits needing very many legs, and these advances are very different from those of the Chilopoda. Some locomotory features of the Geophilomorpha among the centipedes are more nearly primitive than those of any diplopod group (see Part 5) and the slower Geophilomorpha do not run faster than do juliform millipedes of comparable size. *Stigmatogaster* runs more slowly than juliform millipedes with a diplo-segment volume equal to that of two segments (see Table I and p. 337) and *Geophilus longicornis*, one of the fleetest Geophilomorpha reaches a speed of 11 mm. p.sec., which is rather faster than those of corresponding Juliformia (see also

Part 3, Tables 1 and 2). Gaits which are less specialized than those of the Diplopoda and the faster running Chilopoda still persist at the present day, notably in the Symphyla, and will be considered in Part 5.

Many lines of investigation have shown the inappropriateness of the terms 'lower' and 'higher' as applied to functions of animals of very different structure and phylogeny. For example, the circular muscles of the actinian column occupy but a fraction of the thickness that would be required of frog sartorius muscle fibres producing the same tension (Batham & Pantin, 1950). The superiority of the pushing powers of the Diplopoda over those of terrestrial vertebrates of similar size is equally striking (Tables I and II). The lizard and mouse weigh no more than the larger Juliformia and can put out but a quarter of the juliform pushing force. Comparisons with the more powerful Nematophora and Polydesmoidea are even more unfavourable to the vertebrates. Data are not available for a direct comparison of the maximum speeds of a vertebrate such as a lizard and a centipede of equal weight, but it appears probable that the centipede would be much faster, although a British lizard is faster than the smaller *Scutigera*. Animals, however highly specialized in particular directions, are limited by the properties of their living and non-living component parts. Millipedes can only be efficient over a certain range of size, and this range is quite different from that of the vertebrates. The middle part of the curve on text-fig. 6 shows the range over which juliform millipedes are efficient, and as they become larger so their pushing ability falls off. The vertebrates, on the other hand, although less efficient at pushing when their size equals those of millipedes, can become very much larger. Functional relationships set a lower limit to the size of vertebrates, but at a size greatly exceeding that of the lower limit for millipedes.

SUMMARY.

1. An account is given of the locomotory mechanisms and associated structure of a series of millipedes representing the major subdivisions of the Diplopoda, a summary of the data being given in Tables I and II.

2. The Diplopoda in contrast to the Onychophora and other Myriapoda possess a marked ability to push by the motive force of their legs. By this means they achieve either head-on burrowing into leaf mould or pushing by the dorsal surface or a 'flat back' into woodland litter which splits open along one plane, or other specialized ways of life.

3. The habit of curling the body into a protective spiral has been a second habit of major importance in the evolution of the group.

4. Power for pushing is achieved by the use of 'bottom gear' gaits in which the backstroke is of very much longer relative duration than the forward stroke, up to (1— : 9+). These gaits require the presence of very many legs to each metachronal wave, and this has been achieved by the evolution of diplo-segments and many of them. Such gaits are not shown by animals running freely on the surface.

5. Moderate fleetness has been evolved several times, probably in the later stages of diplopod evolution, and gaits with relatively short durations of the backstroke are used, up to (6·7 : 3·3), together with legs which are longer than those of all centipedes other than the Scutigeromorpha, but fast gaits usually appear to be of lesser significance to Diplopoda than the slow powerful gaits. Marked rock-climbing ability occurs in the Colobognatha and Lysiopetaloidae.

6. The skeleto-muscular systems of the trunk region of the several orders are shown to be correlated in great detail with locomotory habits and the several methods of burrowing, and with size. These features comprise the more conspicuous characters of the millipedes, excluding the head, feeding and sensory organs, gonopods and viscera, and are listed on p. 352 (see also p. 329).

.... 7. Specializations exist for strengthening the skeleton; for resisting telescoping at the inter-ring joints; for maintaining mobility, and also rigidity between the hard parts; and for the provision of various types of legs and limb musculature. There are several ways of achieving an acute spiral position, and suitable surfaces for the application of the pushing force. Some of these features appear to be primitive diplopod features, others have been independently acquired by various means in the several groups.

8. The Diplopoda appear to have arisen from Archi-arthropoda, diverging perhaps just after the soft bodied stage, in which a habit of pushing into the substratum was adopted, in contrast to a habit of running round obstacles as envisaged for the ancestors of the Chilopoda (Part 3). The characteristic pushing ability of millipedes could not have been achieved without the evolution of diplo-segments, which allows numerous legs to be carried without the animal becoming proportionately long and thin. Functional reasons are given for the occurrence of a few rings bearing but one pair of legs behind the head.

9. Functional reasons are suggested to account for the evolution of the more conspicuous characters of the several orders, including the respective numbers of trunk segments and differing lengths of legs.

10. The effects of size on structure and on pushing power of millipedes are demonstrated. Structural advances which compensate for a falling off of pushing power in larger millipedes are present.

11. The Diplopoda have the potentiality for efficient burrowing only within certain size limits. The diplopod size range is very different from that of vertebrates, but millipedes of the same size as vertebrates can push much more powerfully.

APPENDIX p. 368.

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DESCRIPTION OF PLATES.

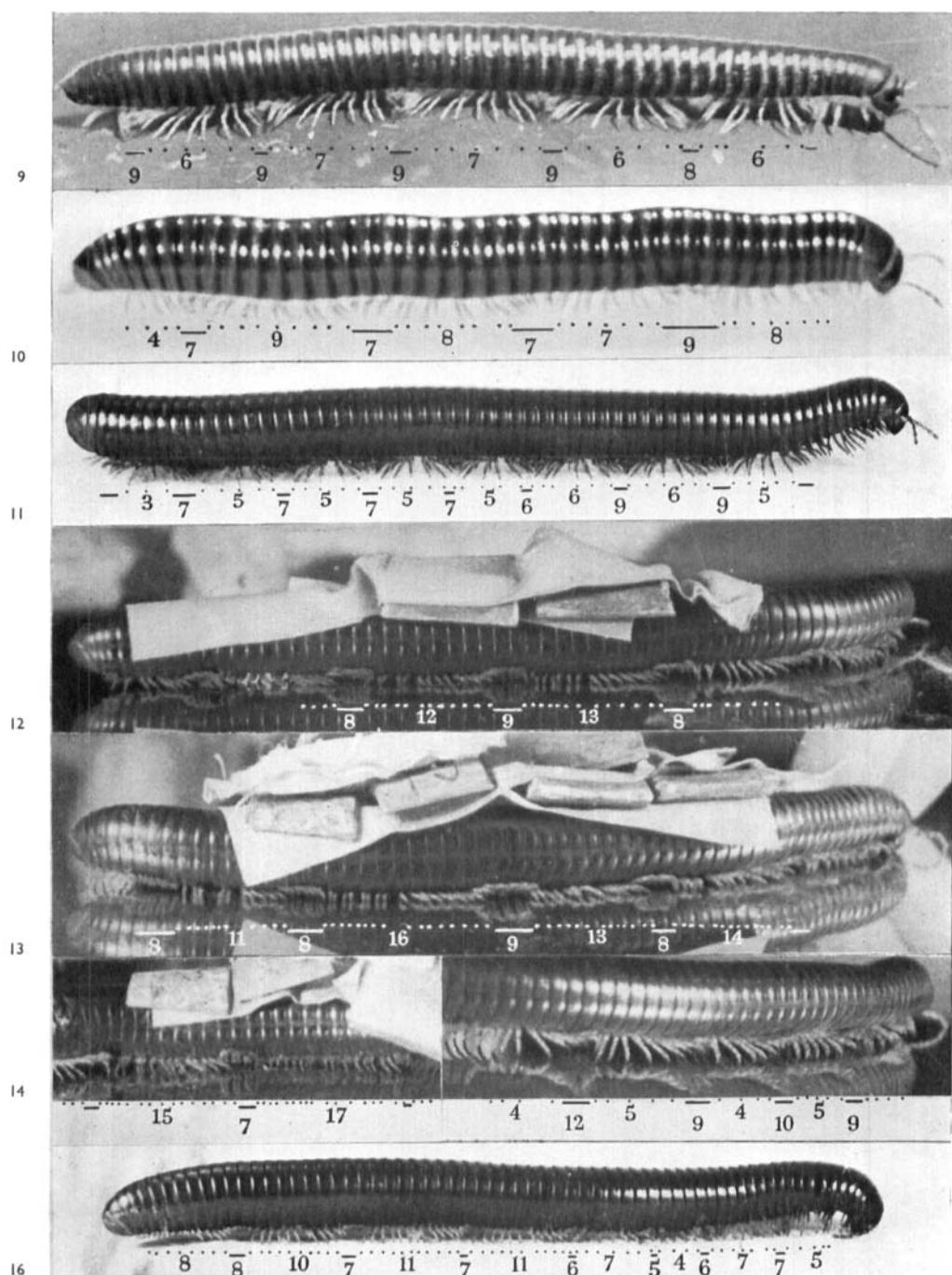
On the plates a black or a white dot near a leg indicates that its tip is on the ground in the propulsive phase. The black or white lines show the positions of each group of legs performing the recovery stroke. The numbers opposite the dots and opposite the lines give the numbers of consecutive legs in the propulsive and recovery strokes respectively in each metachronal wave.

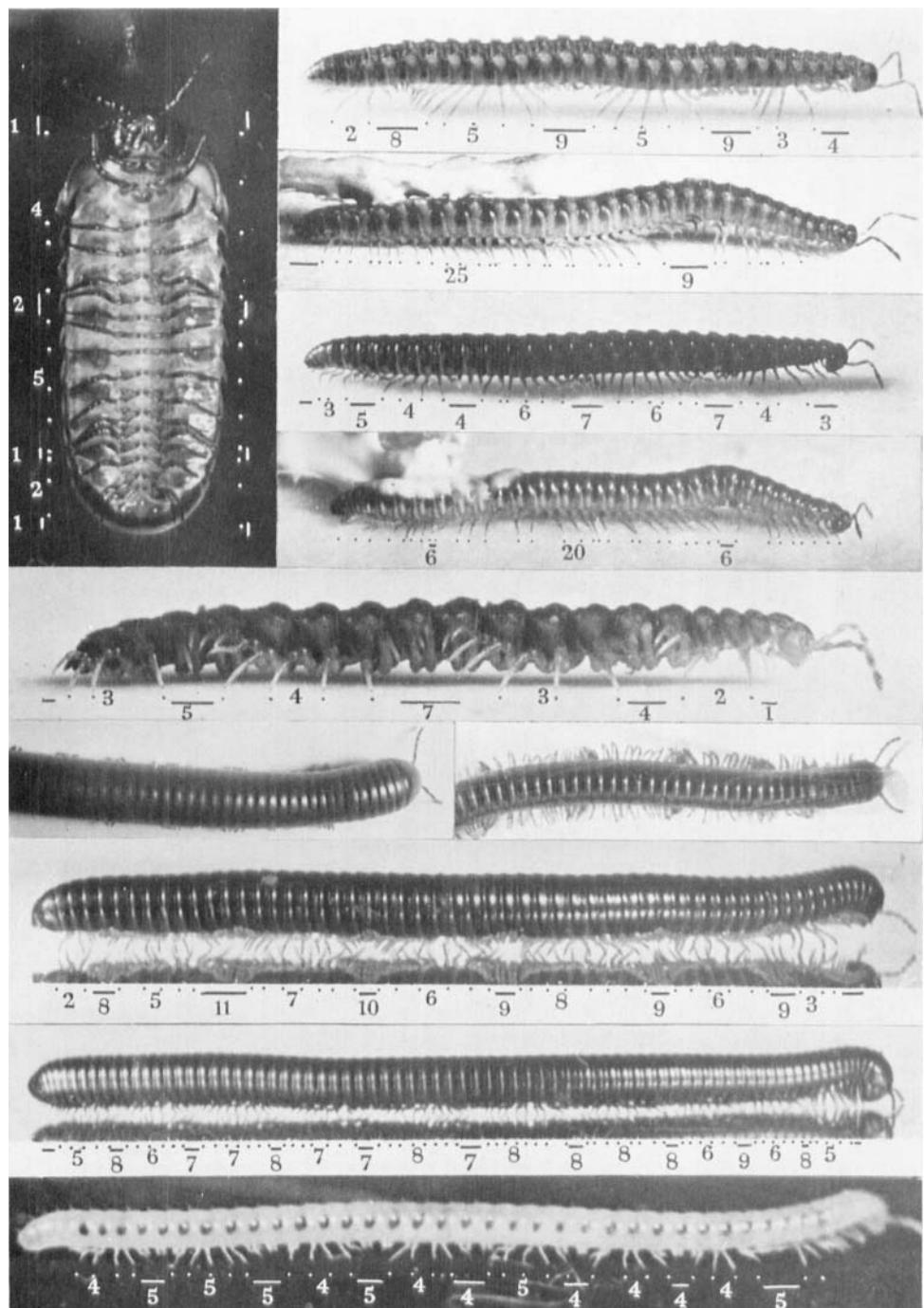
In the legends the figures within the brackets, such as (5·0 : 5·0), give the relative durations of the forward and backward strokes of the gaits shown, and "p.d." signifies the phase difference between successive legs.

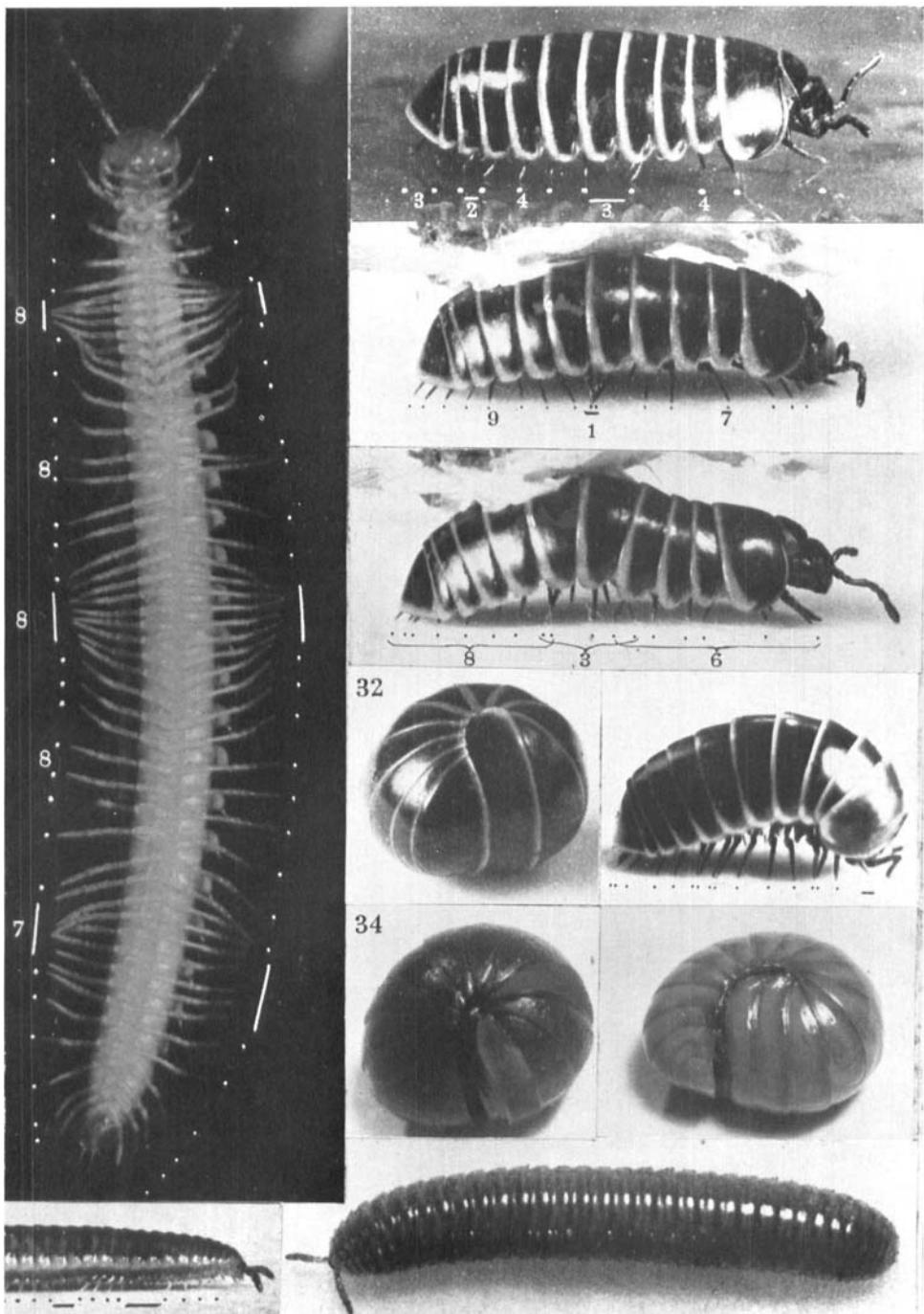
PLATE 52.

FIG. 9. *Schizophyllum sabulosum*, 32 mm., fast free running by gait (5·7 : 4·3), p.d. 0·06 (15-16 legs per wave).

FIG. 10. *Cylindroiulus londinensis* var. *caeruleocinctus*, 38 mm., free running by gait (5·2 : 4·8), p.d. 0·06 (15-16 legs per wave),

*Juliformia*

*Glomeris, Nematophora and Juliformia*



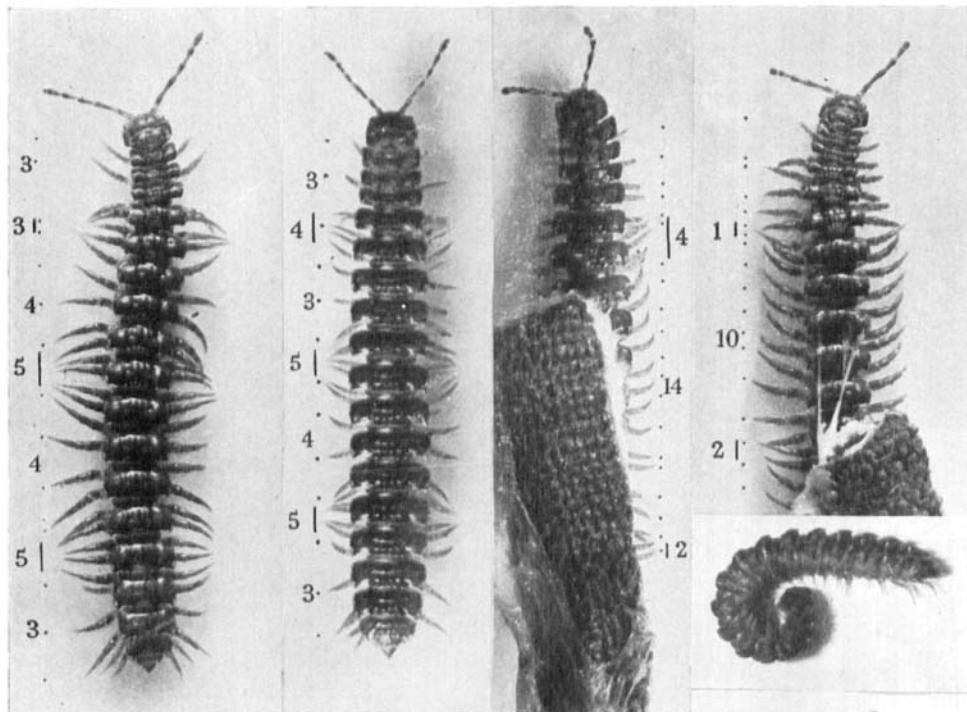
Polymericodon, Glomeris, Sphaerotherium, Glomeridesmus and Polyzonium

38

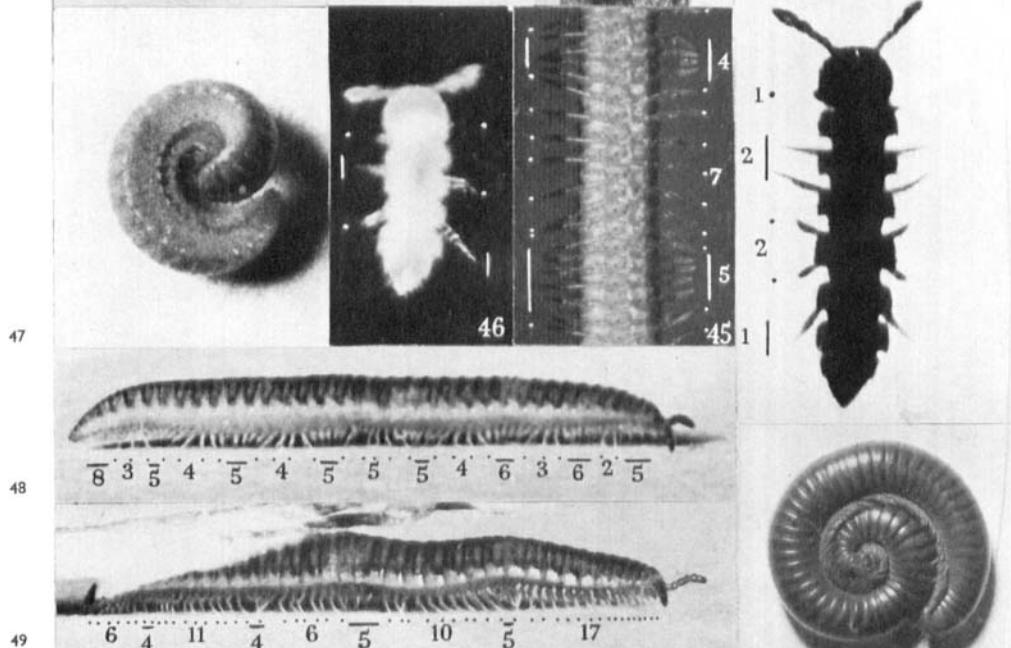
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43

Polydesmus, *Polyzonium* and *Ophistreptus*

- FIG. 11. *Ophistreptus guineensis*, 175 mm., fast free running by gait (5·8 : 4·2), p.d. 0·08 (12–15 legs per wave).
- FIG. 12. *O. guineensis* of 30 gm. weight saddled with 70 gm., gait (4·3 : 5·7), p.d. 0·05 (20–22 legs per wave).
- FIG. 13. *O. guineensis* of 30 gm. weight saddled with 104 gm., gait (3·7 : 6·3), p.d. 0·04 (22–24 legs per wave), two legs lacking on 9th pedigerous ring from the posterior end.
- FIG. 14. *O. guineensis* of 30 gm. weight saddled with 115 gm., gait (2·9 : 7·1), p.d. 0·04 (24 legs per wave).
- FIG. 15. *O. guineensis*, 170 mm., running by fastest gait (6·7 : 3·3), p.d. 0·07 (14–16 legs per wave), mid-ventral line and legs of other side visible in the reflection.
- FIG. 16. *O. guineensis*, 175 mm., pushing, resistance removed, gait (4·2 : 5·8), p.d. 0·06 (18 legs per wave).

PLATE 53.

- FIG. 17. Ventral view of *Glomeris marginata*, 11 mm., freely walking by gait (3·0 : 7·0), p.d. 0·15 (6–7 legs per wave).
- FIG. 18. Oblique lateral view of *Polymicrodon polydesmoides*, 17 mm., running freely by gait (6·0 : 4·0), p.d. 0·08 (12–14 legs per wave).
- FIG. 19. Lateral view of *Polymicrodon polydesmoides*, 18 mm., harnessed to sledge, gait (2·7 : 7·3), p.d. 0·03 (34 legs per wave).
- FIG. 20. Lateral view of *Craspedosoma rawlinsi*, 18 mm., running freely by gait (5·3 : 4·7), p.d. 0·09 (8–13 legs per wave).
- FIG. 21. Lateral view of *Craspedosoma rawlinsi*, 18 mm., harnessed to sledge, gait (2·3 : 7·7), p.d. 0·04 (26 legs per wave).
- FIG. 22. Lateral view of *Polydesmus angustus*, 20 mm., male, running freely, gait (6·6 : 3·4), p.d. 0·1 (9–10 legs per wave). Left legs 1 and 2 visible posterior to right leg 1.
- FIG. 23. Dorsal view of *Ophistreptus guineensis*, 170 mm.
- FIG. 24. Dorsal view of *Plusioporus sulcatus*, 195 mm.
- FIG. 25. *Plusioporus sulcatus*, 195 mm., running freely by gait (6·1 : 3·9), p.d. 0·06 (16–18 legs per wave), reflection shows mid-ventral line and legs of the other side.
- FIG. 26. *Graphidostreptus judaicus*, 135 mm., running freely by gait (5·2 : 4·8), p.d. 0·07 (14–16 legs per wave).
- FIG. 27. *Blaniulus guttulatus*, 15 mm., immature specimen lacking 12 rings, running freely by gait (5·0 : 5·0), p.d. 0·12 (8–9 legs per wave).

PLATE 54.

- FIG. 28. Ventral view of *Polymicrodon polydesmoides*, 17 mm., running freely, gait (6·0 : 4·0), p.d. 0·07 (15–16 legs per wave).
- FIG. 29. *Glomeris marginata*, 14 mm., walking freely by gait (5·7 : 4·3), p.d. 0·15 (6–7 legs per wave). All legs are visible, leg 1 is off the ground and behind leg 2, legs 6–8, 13 and 14 are off the ground, and legs 2–5, 9–12 and 15–17 are propulsive.
- FIG. 30. *G. marginata* harnessed to sledge, gait (1·0 : 9·0), p.d. 0·1 (8–10 legs per wave). All legs visible, leg 8 off the ground, legs 1–7 and 9–17 are propulsive.
- FIG. 31. *G. marginata* harnessed to sledge, gait (1– : 9+), all legs are in the propulsive phase, and probably form three waves, legs 1–6, 7–9 and 10–17, as indicated by the brackets; legs 6 and 7, and 9 and 10, situated at the beginning and end of the waves, cross over because no leg in the recovery phase intervenes. The other visible legs belong to the other side of the body. The hump is not due to the harness.
- FIG. 32. *G. marginata* rolled up, anterior end to the right, posterior tergites overlap the anterior (left) edge of fused 2nd and 3rd tergites (shield).
- FIG. 33. *G. marginata* in the pushing position (resistance removed), leg 1 off the ground, succeeding legs propulsive, leg 17 not visible.
- FIG. 34. *Sphaerotherium dorsale*, 35 mm., dead specimen rolled up, anterior end to the right, posterior tergites overlapping anterior (left) edge of 2nd tergite.
- FIG. 35. *Glomerideemus mexicanus*, 46 mm., dead specimen rolled up, anterior end to the right, posterior tergites overlapping the anterior (left) edge of 4th tergite.
- FIG. 36. Anterior end of *Polyzonium germanicum*, 11 mm., running freely, gait (6·4 : 3·6) showing the head.
- FIG. 37. *Polyzonium germanicum*, 11 mm., in dorsal view.

PLATE 55.

- FIG. 38. *Polydesmus angustus*, 20 mm., male, running freely by gait (5·5 : 4·5), p.d. 0·12 (9 legs per wave).
- FIG. 39. *Polydesmus angustus*, 20 mm., female, running freely by gait (5·9 : 4·1), p.d. 0·11 (8–9 legs per wave).
- FIG. 40. *Polydesmus angustus*, 20 mm., female, harnessed to sledge, gait (2·2 : 7·8), p.d. 0·04 (18 legs per wave). Right legs 8–11, 26 and 27 off the ground.

- FIG. 41. *Polydesmus angustus*, 20 mm., male, harnessed to sledge, gait (1·6 : 8·4), p.d. 0·08 (12 legs per wave). Left legs 8, 10 and 20 off the ground.
- FIG. 42. *Polydesmus angustus*, 18 mm., female, closest spiral position.
- FIG. 43. *Polydesmus angustus*, second larva, 2·1 mm., gait (5·0 : 5·0), p.d. 0·25 (4 legs per wave).
- FIG. 44. *Ophistreptus guineensis*, 175 mm., spiral position.
- FIG. 45. Ventral view of the middle part of *Craspedosoma rawlinsi*, 18 mm., gait (4·5 : 5·5), p.d. 0·8 (12 legs per wave).
- FIG. 46. *Polydesmus angustus*, first larva, 1·16 mm., gait (3·5 : 6·5), p.d. 0·4.
- FIG. 47. *Polyzonium germanicum*, 11 mm., spiral position.
- FIG. 48. *Polyzonium germanicum*, 11 mm., running freely, gait (6·4 : 3·6), p.d. 0·1 (9–10 legs per wave).
- FIG. 49. *Polyzonium germanicum*, 11 mm., harnessed to sledge, gait (2·6 : 7·4), p.d. 0·08 (10–15 legs per wave).

A P P E N D I X

Since this paper was written, H.-E. Gruner's work (1953, *Der Rollmechanismus bei kugelnden Land-Isopoden und Diplopoden*, *Mitt. Zool. Mus. Berlin*, **29**, 148–179) has been published. He shows how the rolling up in Isopoda is effected by a body which is half cylindrical in section; the sternite joints are practically hinges, and the dorsal overlap of the tergites is as great as in the Oniscomorpha, so allowing a large amount of dorsal expansion. Gruner's text-fig. 4 *a* shows diagrammatically how tergites overlapping from before backwards and sternites overlapping from behind forwards must fix the transverse axis of the nodding movement low down, at the junction of tergites and flat sternites. Gruner contrasts this unusual jointing with that found in the Diplopoda shown in his fig. 4 *a*.

In the Oniscomorpha, however, the sternites also overlap one another from behind forwards (see text-figs 4 *c* and *d* shown here and p. 317) and, if the tightest coil is to be achieved, the axis of movement between successive rings also needs to be maintained at the level of the ventral surface of the half-cylindrical body (see text-figs. 1 *a* and 4 *d* and *e* shown above). Gruner's fig. 4 *a* supplies the functional explanation for the forward overlap of the sternites of the Oniscomorpha also.

A forward overlapping of sternites in the Oniscomorpha probably evolved from a primitive condition, as is seen today in *Polyzonium*, where there is no overlap of successive sternites in either direction on dorso-ventral bending (p. 357), and arose in association with a perfection of rolling up by a reduction of the body to a half cylinder and a utilization of the mobility of the ventral exo-skeleton (pp. 315 and 338). The opposite overlap of sternites from before backwards in the Juliformia, Polydesmoidea and Nematophora is necessitated by the cylindrical form of their bodies (text-fig. 1 *a*) and the direction of overlap of their tergites.