PATTERNS OF SECONDARY GROWTH AND A REVISION OF THE SYSTEMATICS IN *MICROCOTYLOIDEA* AND *GASTROCOTYLIDAE* (MONOGENOIDEA)

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(With 7 Text-figures)

CONTENTS

I—INTRODUCTION

An analysis of the dynamics of axial growth potentials in the hind-body of the higher Monogenoidea, particularly those showing secon-

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dary growth, was suggested by the wealth of the variety displayed in recently discovered forms from fishes in tropical seas. This naturally led to a re-examination of their relationships.

The systematic scheme presented here for the higher monogeneans is consciously a temporary one, and its main feature is the re-introduction of superfamily taxa, absent in the welcome expansion of the scheme by Bychowsky. Bychowsky (1957) provided three orders each for the subclasses Polyonchoinea Bych., 1937, and Oligonchoined Bych., 1937, and the order Mazocraeidea Bych., 1957 has 7 families. I agree with the American workers (Hargis, 1959, Price, 1959) that superfamilies are again necessary to accommodate the strange variety of forms discovered since Bychowsky's great work went to press. I have suggested 6 superfamilies for Discocotylinea, and elaborated the schemata for two of them: Microcotyloidea (Unnithan, 1957) *s. str. emend.*, in respect of the families *Axinidae* Unnithan, 1957 and Heteromicrocotylidae (Yamaguti, 1963) *s. str. emend* (an analysis of the Microcotylidae *s. str.* will follow), and Gastrocotyloidea Price, 1959, in respect of Gastrocotylidae (a study of Opisthogynidae Unnithan, 1962 appears elsewhere).

The revision is an attempt to rationalize the classification in the light of comparative anatomy of the clamps, and also of an analysis of the dynamics of the axial growth potentials of the haptoral region. The opportunity has been taken to make some corrections in the out-of-date synopsis of Sproston (1946), and to clarify and emend certain definitions in the paper on Axinidae (Unnithan, 1957): in this, only passing reference was made to the systematics of species related to the new forms, even when they were affected by recent findings. Accordingly, each species has been reconsidered at lengths proportionate to their interest in the present inquiry. Substantial contributions on Monogenoidea by Price (1962) and Yamaguti (1963) have appeared since the first draft of this paper was ready. Though their rationale is on different lines, portions found to be helpful from these two have also been incorporated in the present paper.

Note on terminology: 'Haptor' is used in preference to Dawes' 'opisthohaptor' for the whole of the posterior adhesive complex in all Monogeneoidea ; *'Protohaptor'* for the ventral terminal lobe of the larval haptor bearing two dissimilar pairs of anchors and usually a terminal pair of larval hooklets: all or some of these structures may be retained by the adults. The *'euhaptor'* is the definitive haptor of the adult, and in forms without secondary growth comprises only the remodelled larval haptor, but in forms with secondary growth includes in addition all clamp-bearing regions produced by anadromous metamerism. *'Metahaptor'* is an anterior extension of the euhaptor, ventrally to the body axis and bearing clamps produced by a katadromous metamerism from the anterior side of the dichotomized formative zone —the euhaptor being formed from the posterior moiety of this zone. The metahaptor may be a unilateral flange or a bilateral lobe, always physically if not qualitatively continuous with the euhaptor.

MICROCOTYLOIDEA (Unnithan, 1957) *s. str. emend.*

The present emendation is the removal of Gastrocotylidae from the superfamily as constituted by Unnithan (1957: 41). The superfamily is now defined as Discocotylinea Bychowsky, 1957, in which the clamps are basically discocotylid, with no extra sclerites entering into their essential mechanism, and in which there is a secondary replication of the four primary pairs of clamps of the larval haptor: the growth of the euhaptor so formed is potentially unlimited throughout life.

II — SOME PATTERNS OF SECONDARY GROWTH IN THE HAPTOR OF MICROCOTYLOIDEA (AND GASTROCOTYLIDAE)

The potentially unlimited growth of the euhaptor may be modified by secondary inhibitory influences operating differentially in the various growth-axes of the euhaptor, being imposed along the body/haptor-axis, either, or both, of the lateral longitudinal replication axes; or more rarely, along the lateral (transverse) axes of the haptor itself. These inhibitory influences are responsible for the more striking degrees and kinds of asymmetry of the haptor. In addition, there may be secondary stimulative influences along these axes, inducing both qualitative and quantitative changes in growth. These positive influences are less evident in those axes where negative influences have been strong. Secondary stimulation is usually persistent in an axis, at its original intensity, both qualitatively and quantitatively. If this involves remodelling of the clamp sclerites at some level of the axis, the new form appears abruptly — except where the remodelling is extreme, as in Pyragraphorinae, where it is gradually developed. Stimulative effects, once achieved, are maintained in subsequent replications: in contrast to inhibitory effects which, unless they are absolute at the outset, increase gradually along the growth axis, *e.g. Heteraxine* spp. clamps of the short row are formed in a gradually diminishing series, and are produced more and more slowly compared with the less inhibited row.

Quantitative stimulation has two manifestations: (*a*) the clamps themselves increase in size, and (*b*) there is an accelerated replication rate, and this is nearly always accompanied by a *dichotomy of the axes of growth.* This is necessary after a certain threshold of stimulation, since a haptor growing much faster than the body/haptor-axis would lack space for development.

In the simplest instances this does not occur till late in life (proximal region of the haptor), when there is a longitudinal scission in the formative zone, resulting in a *lateral dichotomy* of the axis of replication (perhaps irrevocably), so that two clamps are formed side by side instead of in single file: *e.g.* in *Microcotyle priacanthi* Meserve, *M. pomatomi* Goto: (and in Gastrocotylidae, *Chauhanea madrasensis* Ramalingam, *Gotocotyla secunda* (Tripathi) etc. In all these and in similar instances of lateral dichotomy in the proximal (younger) sector of the euhaptor-rows, the stimulus is bilateral, but in instances of a second dichotomy in the same plane, resulting in three parallel rows, this may not occur at the same level on both flanks, or one flank may not have a secondary or tertiary dichotomy at all; but more data are required to confirm this. It seems to be a character of secondary stimulation (accelerated growth) to affect both lateral axes equally, or to be discernible on one side only: no example appears to be known of a marked acceleration on one side, and a minor (similarly abrupt) acceleration on the other, a character in marked contrast to the manifestations of inhibitory influences.

A more highly evolved expression of growth stimuli is seen in the metahaptor: a secondary haptoral lobe produced anteriorly to the euhaptor and growing forwards (morphologically) ventral to the body proper. Functionally, as a postural effect, the body is pivoted more or less at right angles to it, and away laterally in the vertical plane, in the direction of the cibo-respiratory current over the gill-surface of the fish-host: an habitual posture of all larger monogeneans. This fact is well known, but has been nicely illustrated by Llewellyn (1956 *a*: 113) though it was probably outside the intended scope of his paper to emphasize that the resulting torque on any organs in the hind-body embraced by the haptoral frills or flanges, is often effective in bringing about significant displacements among them, and also relative to the body-axis. *Somatic asymmetry* occurs when the pivoting axis is within the gonad-zone, the least resilient part of the body; this is more marked when the body/haptor axis is shortened or aborted, that is, when the euhaptor flanges are adherent to the sides of the body, *e.g.* in *Thoracocotyle ovalis* Tripathi. A thickened cuticle and body-wall developed in Vallisiinae and Protomicrocotylidae are additional causes for their gross asymmetry in the gonad-zone (all these are Gastrocotyloidea).

In the simple euhaptor, the first secondary clamps are produced from a formative zone immediately anterior to the proximal (most anterior) pair of primary clamps, as is shown conclusively in Bychowsky's figures (1957: figs. 252, 253) of *Prosomicrocotyla gotoi.* Thus, throughout life, new clamps are added at the anterior end of the euhaptor. When there is a dichotomy and a dual zone of replication is formed, however, the secondary clamps forming anterior to this are pushed over ventrally and anteriorly, and particularly if the dichotomy has affected both lateral axes, they carry with them part of the median axial tissues of the haptor, and a bud is formed. The type of tissue or organ carried outwards in the metahaptoral bud is, of course, dependent on the depth of the dichotomy organoleptically.

The level of the dichotomy in the larval haptor can be found at any time by counting the number of diminutive clamps on the anterior end of the metahaptor. In highly modified clamp forms, the number on the posterior end of the euhaptor may be more difficult to assess, nor are we certain that in some cases the posterior primary clamps are not lost with the protohaptor — the lappet bearing the larval anchors, the loss of which occurs spasmodically in genera throughout the order Mazocraeidea Bychowsky, 1957. In the extreme instance of *Pricea* spp. (Gastrocotyloidea: (Gastrocotylidae) the dichotomy evidently takes place in the proto-haptoral zone of the larval haptor., and between the two pairs of anchors. This is witnessed by the presence of the proximal pair of anchors on the end of the body proper, at the level where the metahaptor leaves it. They remain attached (*in situ*) owing to their longitudinal muscles being continued into the body proper. The shallowness of the dichotomy in this group involves only the more superficial tissues, as it does in some species of *Microcotyle sensu lato.*

Though the euhaptor and metahaptor grow out from juxtaposed formative zones, they are immediately separate entities, and nearly always seem to show a different degree of acceleration of axial growth: sometimes the euhaptor is the longer as in *Pricea,* and perhaps *Microcotyle cepolae* Yamaguti (1938: xix, fig. 32), and *M. gimpo* Yamaguti (1958: liii, fig. 15); sometimes about equally long as in *Pyragraphorus pyragraphorus* (Mac Callum & Mac Callum, 1913), and perhaps in *Microcotyle branchiostegi,* Yamaguti (1938: xvii., fig. 1) *M. sebastisci* Yamaguti (1938: xvii, fig. 13); but sometimes the metahaptor has a sustained higher growth acceleration than the euhaptor, as in *Hargisiella hippos* (Hargis, 1956: x, fig. 19) gen. n., also in the unilateral metahaptor of *Cemocotyle carangis* MacCallum, 1913), and perhaps in *Microcotyle leiognathi* Tripathi (1959, fig. 53). In *Microcotyle (sensu lato)* spp. just mentioned, there is no qualitative difference in the clamps of the metahaptor, nor is there in *Hargisiella* or *Pricea,* but the secondary stimuli producing the metahaptor in *Pyragraphorus* are accompanied by other positive influences which cause an extreme remodelling of the clamps, and the same is true to a lesser degree in *Cemocotyle, Xureliphilus elongata* (Meserve, 1938, figs. 53, 57) gen. n., and *Tripathiana minuta* (Tripathi, 1959, fig. 55) the last three having only a unilateral metahaptor.

In Microcotyloidea: Axinidae, characterized by various degrees of inhibition exerted on their potentially unlimited clamp replication, it is not surprising that when these inhibitory influences are exerted at least on one of the clamp-rows, the other row is so far never known to receive a secondary stimulation. And when the inhibition (total) is exerted only on the median body-haptor axis, as in Axininae Unnithan, there is only a slight differential inhibition exerted on the lateral replication axes (except in *Oligapta* Unnithan, where it is equally strong). There is one very interesting instance in Axininae of the development of a unilateral metahaptor namely in *Chlamydaxine truncata* (Hargis, 1956 : xi, fig. 5), (Unnithan, 1957, fig. 4) at first glance difficult to interpret, because owing to the total inhibition of the longitudinal axis of the haptor/body but not of the "longitudinal" clamp-replication axes, the clamps accumulate in two lateral rows, the formative zone turning ventral to the larval haptor: at least the anchors (protohaptor) persist (always on the dorsal side of the adult haptor, (Unnithan, 1957: 82, 88, 101, 114). As a further complication in *Chlamydaxine,* there has been a unilateral dichotomy of the formative zone on one side, resulting in a short ventral lobe turning anteriorly, bearing much larger clamps as it does so. An interesting point here is that as a result of this secondary stimulation, the metahaptor has overcome the inhibition on longitudinal growth, and carries the deeper body-organs, intestinal rami and a few vitellaria forwards with it.

The secondary growth rhythms, in the haptor of Microcotyloidea, including their inhibitions and stimulations as discussed above, apply also to the definition of Gastrocotyloidea: Gastrocotylidae, which also have a potentially unlimited power of clamp replication. But there is a fundamental difference (or one which is not a dynamic character in the growth-vector sense, but is qualitative and therefore more appealing to comparative morphologists) and this consists of the presence of at least one pair of extra sclerites in the clamp capsule, at least originally playing an essential role in the clamp mechanism. These are the oblique braces in the posterior (distal) part of the capsule in Gastrocotylinae, Priceinae, and Gotocotylinae: in Thoracocotylinae they are jettisoned from the capsule which has become remodelled as a clamp-sucker but they persist along with the dorsal jaw rami outside its effective frame (Text-fig. 6 A-G). Other sclerites are developed in other subfamilies, from rudiments which are frequently to be seen in even the simple microcotylid clamps of Microcotylidae and Axinidae, but where they play no essential part in the mechanics of the clamp.

In families without this secondary replication of the primary four pairs of clamps, namely families in which the clamp pairs are limited to the four pairs of the larval haptor, the clamp structure becomes a more important taxonomic criterion. In fact it is true, that in general, those having extra sclerites of the basic "gastrocotylid type of clamp" do have other uniting (somatic) characters in combinations not found in the simpler Discocotylinea, and in general they are apparently more highly evolved.

Moreover, Gastrocotyloidea are more frequently (but by no means always) found on the more highly evolved families of fishes, a characteristic shared by the most highly evolved Microcotyloids, the Heteromicrocotylidae. Soviet colleagues have pursued many ramifications of the hypothesis of the host/parasite parallelism in evolution, and have even ventured to attribute various parasites, including Monogenea, to their putative geological horizon *vis-a-vis* the fossil evidence for their present-day hosts, on the one hand, and on the other, the propinquity in the relationships of the known species of parasites of correspondingly related genera of fishes. The generally accepted rule is that the parasite evolves less rapidly than the host, but in many instances it could be cited that the reverse may be true, at least for Monogenea, where two or more related species are found in the same host exclusively of other "likely" hosts elsewhere. Whereas in other instances we certainly have some very archaic forms living to-day on descendents of very primitive fish stocks, I am more inclined to lay stress on Dollfus' warning (1957 : 184, 269; and elsewhere) that parasites of primitive fishes are by no means always primitive, and the corollary that infection by a relatively modern stock may have taken place in relatively recent geological times. Environmental propinquity of historically very different hosts, particularly if these are shoaling in rather closed waters may, chiefly for statistical reasons, favour the establishment of a new host-parasite relationship.

III—THE REINTRODUCTION OF SUPERFAMILIES INTO THE SYSTEMATIC SCHEME OF DISCOCOTYLINEA BYCHOWSKY 1957

The peculiar characters of secondary growth revealed by some well-known, and several newly discovered, members of this suborder are herein considered, criteria of taxonomic rank second only to basic clamp-architecture.

Accordingly, the superfamily Microcotyloidea, *sensu emend. nov.* represents forms with secondary haptoral growth involving clamps of the simple 'discocotylid' type, and Gastrocotylidae *sensu emend.* those with 'gastrocotylid' clamps (with additional sclerites in their mechanism). The difference in taxonomic rank is due to the exigencies of the logical scheme of the suborder, accepted provisionally pending further knowledge of the ontogenies of Gastrocotyloidea Price, 1959.

Since the first draft of this paper was written, I have found support for the reintroduction of superfamilies in papers by Hargis (1959) and Price (1959), the latter already having erected my intended Gastrocotyloidea, though its internal grouping is unlike the present, its criteria based on additional clampsclerites, are identical. Price makes no mention of Bychowsky's works, and his rationale is not clear when he unites genera with limited haptoral growth in the same family with *Gastrocotyle,* (those now placed in the new family Opisthogynidae Unnithan, 1962); moreover, he retains Priceinae Chauhan, in its original context, thus separating *Pseudaxine* from *Neothoracocotyle,* and *Thoracocotyle* from *Amphipolycotyle,* pairs of genera with fundamentally similar clamps.

While emphasizing the importance of the pattern of growth-potentials throughout the haptoral region, I have given prior taxonomic rank to basic clamp-type, preserved at superfamily level, since it is the main criterion for the higher taxa of the subclass Oligonchoinea Bychowsky, 1937. Consistency appears to fail in the case of Protomicrocotylidae Poche, since recent authors have described species of *Protomicrocotyle, sensu lato,* with sometimes microcotylid and sometimes gastrocotylid clamps; for this reason, and for the peculiar somatic asymmetry and unique haptor, I reserve a separate superfamily for it (see Unnithan, 1962). For logical consistency, I have raised three other of Bychowsky's family groups to superfamily rank. His 1957 scheme, with these emendations for Discocotylinea is set out below.

Class: MONOGENOIDEA (Beneden) Bychowsky, 1937.
  Subclass: *POLYONCHOINEA* Bychowsky, 1937.
    Order: DACTYLOGYRIDEA Bychowsky, 1937.
      Suborder: *DACTYLOGYRINEA* Bychowsky, 1937.
        Family: DACTYLOGYRIDAE Bychowsky, 1933.
          Subfamily: DACTYLOGYRINAE Bychowsky, 1933.

Subfamily: ANCYROCEPHALINAE Bychowsky, 1937.
Subfamily: LINGUADACTYLINAE Bychowsky, 1957.
Family: DIPLECTANIDAE Bychowsky, 1957.
Subfamily: DIPLECTANINAE Monticelli, 1903.
Subfamily: RHAMNOCERCINAE Monaco, Wood & Mizelle, 1954.
Family: PROTOGYRODACTYLIDAE Johnston & Tiegs, 1922.
Family: CALCEOSTOMATIDAE (Par. & Per. 1890) Price, 1937.
Suborder: *MONOPISTHOCOTYLINEA* (Odhner, 1912) Bychowsky, 1937.
Family: MONOCOTYLIDAE Taschenberg, 1879.
Subfamily: MONOCOTYLINAE Gamble, 1896.
Subfamily: DASYBATOTREMINAE Bychowsky, 1957.
Subfamily: CALICOTYLINAE Monticelli, 1903.
Subfamily: MERIZOCOTYLINAE Johnston & Tiegs, 1922.
Family: LOIMOIDAE Bychowsky, 1957.
Family: DIONCHIDAE Bychowsky, 1957.
Family: CAPSALIDAE Baird, 1853.
Subfamily: CAPSALINAE Johnston, 1929.
Subfamily: MEGALOCOTYLINAE Bychowsky, 1957.
Subfamily: TROCHOPODINAE (Price, 1936) Sproston, 1946.
Subfamily: ENTOBDELLINAE Bychowsky, 1957.
Subfamily: ENCOTYLLABINAE Monticelli, 1892.
Subfamily: NITZSCHIINAE Johnston, 1931.
Family: ACANTHOCOTYLIDAE Price, 1936.
Subfamily: ACANTHOCOTYLINAE Monticelli, 1903.
Subfamily: ENOPLOCOTYLINAE Tagliani, 1912.
Family: MICROBOTHRIIDAE Price, 1936.

Order: TETRAONCHIDEA Bychowsky, 1957.
Family: TETRAONCHIDAE Bychowsky, 1937.
Family: AMPHIBDELLATIDAE (Carus, 1885) Bychowsky, 1957.
Family: TETRAONCHOIDIDEA Bychowsky, 1951.
Family: BOTHITREMATIDAE Bychowsky, 1957.

Order: GYRODACTYLIDEA Bychowsky, 1937.
Suborder: *GYRODACTYLINEA* Bychowsky, 1937.

Family: GYRODACTYLIDAE (v. Ben. & Hesse, 1863) Cobbold, 1864.
Suborder: *POLYOPISTHOCOTYLINEA* (Odhner, 1912) Bychowsky, 1937.
Family: POLYSTOMATIDAE (Carus, 1936) Gamble, 1896.
Family: SPHYRANURIDAE Poche, 1926.
Subclass: *OLIGONCHOINEA* Bychowsky, 1937.

Order: DICLYBOTHRIIDEA Bychowsky, 1957.
Family: DICLYBOTHRIIDAE Bychowsky & Gussew, 1950.
Family: HEXABOTHRIIDAE Price, 1942.

Order: CHIMAERICOLIDEA (Brinkmann, 1952) Bychowsky, 1957.
Family: CHIMAERICOLIDAE Brinkmann, 1942.

Order: MAZOCRAEIDEA Bychowsky, 1957.
Suborder: *PTERINOTREMATINEA* Bychowsky & Nagibina, 1959.
Family: PTERINOTREMATIDAE Bychowsky & Nagibina, 1959.
Subfamily: PTERINOTREMATINAE Caballero & Bravo Hollis, 1955.
Suborder: *MAZOCRAEINEA* Bychowsky, 1957.
Family: MAZOCRAEIDAE Price, 1936.
Family: HEXOSTOMATIDAE Price, 1936.
Suborder: *DISCOCOTYLINEA* Bychowsky, 1957.
Superfamily: DISCOCOTYLOIDEA superfam. nov.
Family: DISCOCOTYLIDAE (Price, 1936) Tripathi, 1959.
Family: DIPLOZOOIDAE Tripathi, 1959.
Superfamily: PLECTANOCOTYLOIDEA superfam. nov.
Family: PLECTANOCOTYLIDAE Poche, 1926.
Superfamily: DICLIDOPHOROIDEA (Price, 1936) *sensu stricto*, emend.
Family: DICLIDOPHORIDAE Fuhrmann, 1928.
Superfamily: MICROCOTYLOIDEA (Unnithan, 1957) *s. str.*, emend.
Family: MICROCOTYLIDAE (Taschenberg, 1879) *s. str.*, emend.

Family: AXINIDAE Unnithan, 1957.
Subfamily: AXININAE Monticelli, 1903.
Subfamily: HETERAXININAE Unnithan, 1957.
Subfamily: MONAXININAE Unnithan, 1957.
Family: HETEROMICROCOTYLIDAE (Yamaguti, 1963) *s. str.*, emend.
Subfamily: HETEROMICROCOTYLINAE subfam. nov.
Subfamily: CEMOCOTYLINAE subfam. nov.
Subfamily: PYRAGRAPHORINAE subfam. nov.
Superfamily: PROTOMICROCOTYLIOIDEA Unnithan, 1962.
Family: PROTOMICROCOTYLIDAE Poche, 1926.
Sumfamily: PROTOMICROCOTYLINAE Johnston & Tiegs, 1922.

Subfamily: ABORTIPEDINAE Unnithan, 1962.
Subfamily: LETHACOTYLINAE Unnithan, 1962
Superfamily: GASTROCOTYLOIDEA Price, 1959.
Family: GASTROCOTYLIDAE Price, 1943.
Subfamily: GASTROCOTYLINAE (Sproston, 1946) *s. str.*, emend.
Subfamily: THORACOCOTYLINAE subfam. nov.
Subfamily: PRICEINAE (Chauhan, 1953) *s. str.*, emend.
Subfamily: ENGRAULICOLINAE subfam. nov.
Subfamily: GOTOCOTYLINAE subfam. nov.
Family: ANTHOCOTYLIDAE Bychowsky, 1957.
Family: OPISTHOGYNIDAE Unnithan, 1962.
Subfamily: OPISTHOGYNINAE Unnithan, 1962.
Subfamily: PENTATRINAE Unnithan, 1962.
Subfamily: VALLISIINAE (Price, 1943) *s. str.*, emend, in Unnithan, 1962.
Family: GEPHYROCOTYLIDAE Unnithan, 1966.

The emendations made in the families Axinidae, Heteromicrocotylidae, and Gastrocotylidae in this paper, and in Opisthogynidae Unnithan (1962), elsewhere, (erected for gastrocotyloid worms with no additions to the 4 primary pairs of clamps, and in which the ovary lies behind the main testicular zone), are open to criticism in their being perhaps too "open": several genera, for example, are monotypic. My defence is that the great variety of structure presented by these newly discovered forms demands taxonomic separation to at least the degrees suggested, when the array is compared with the degrees of structural variation found in Polyonchoinea. The rate at which new genera are being discovered, now that attention is directed to fishes of tropical waters in various parts of the world, would suggest that only a tithe of existing forms are yet known. Considering the narrow host-specificity of Monogenoidea and that many host-species harbour four or more different monogeneans, added to the fact that there are over 20,000 species of fishes known to science, the great majority of which have not been searched for monogeneans, the present attempts to expand the systematic schemata may very soon appear less extravagant.

In the sections which follow, each family (and in Gastrocotylinae, subfamily) will be preceded by a general discussion of the range of structural variation it displays, evolutionary trends in modifications of the basic clamp-sclerites, and peculiarities in secondary growth phenomena, where of particular interest generic characters are similarly reviewed. All species known to me are cited, usually with some diagnostic notes; several emendations are made in orthography of specific names consonant with their present genus, and some corrections have been made in host-nomenclature. Only recent synonyms are cited: several, in some American and Indian publications, being due to inadequate proof-correction, a remediable source of confusion.

IV — SECONDARY GROWTH PHENOMENA AND CLAMP MODIFICATION AS SYSTEMATIC CRITERIA

MICROCOTYLOIDEA Unnithan, 1957, *sensu stricto:* Discocotylinea, in which there is a potentially unlimited replication of the clamps, which are basically of discocotylid type.

MICROCOTYLIDAE Taschenberg, 1879, *s. str.*—Microcotyloidea, in which the usually very numerous clamps are small and delicate versions of the typical discocotylid clamp. Very rarely there is a slight secondary inhibition in the replication, and the two lateral axes are practically equally affected, but a secondary stimulus is far more common. Quantitatively, in the clamps themselves, there may be an increase in size anteriorly in the series ; rarely, a stimulus for qualitative change — an adaptive remodelling of the abaxial jaw-rami, so that the right and left counterpart clamps are mirror-images, as in *Microcotyle mormyri* Lorenz—discovered by Bychowsky (1957, fig. 309). Quantitative replication-stimuli are frequently imposed, sometimes late in life there is a lateral dichotomy in the axes, when two or more rows of clamps are formed along each side of the more proximal (anterior) region of the euhaptor. The double row on each side of *M. pomatomi* Goto, 1900, has been confirmed by Hargis (1956, X: 440). The euhaptor is practically symmetrical in all species — the shorter side never having less than 90% of the clamps of the longer : greater discrepancies in number, and in length of sides have been transferred to Axinidae as evidence of an arbitrarily significant secondary differential inhibition. Sometimes there is an earlier and stronger replication stimulus resulting in an anterior-posterior dichotomy of the replication-axes, involving more or less of the body-haptor axis medially, so that a firm metahaptor is formed: its growth-rate differing more or less from that of the euhaptor, but it is always bilaterally symmetrical. There is a great diversity in the form of the genital terminalia, but the ovary is always pretesticular and its distal limb descends, often forming a double arch. The protohaptor never persists in the adult. The sub-family taxa have been studied in detail for the whole range, including some new tropical species (cf. Unnithan, 1967). At present it is necessary to mention only two groups of transitional species : (1) Replication-stimulus is weak on both lateral axes (the number of clamps on each side in parenthesis) in *Microcotyle trachini* Par. & Per., 1889, from *Trachinus radiatus* (8-10) and in Bychowsky, 1957, fig. 308 (8 each side, increasing gradually in size proximally) ; *Diplasiocotyle johnstoni* Sandars, 1944, from the mullet *Agonostomus forsteri* (7 pedunculated) ; and in *M. truncata* Goto, 1894 — now placed in Gastrocotylinae in the new genus *Yamaguticotyla* Price, 1959, from *Pristipoma japonicum* (10) and *Parapristipoma trilineatum* (11).

(2) Transition to Heteraxinae-type of haptor, showing unequal stimuli for clamp-replication in the two axes is expressed here by the numerical percentage of the shorter to the longer row. There is, however, no evidence of inhibition in any of these instances, the clamps are neither absolutely nor progressively smaller in the shorter row, so I interpret this condition as differential stimulation: *Microcotyle heteracantha* Manter, 1938, from the sciaenid *Cynoscion nebulosus* (according to Hargis 1956, X: 438, on *C. regalis* also) — 84% — 89% ; *M.*

pseudoheteracantha Hargis, 1956 (X: 440) from *Cynoscion nothus*—according to his fig. 1, about 87% ; *M. pamae* Tripathi, 1956, from *Pama pama,* a fluviatile sciaenid — 82%—84.5%. All these from sciaenids have a single filament on the egg, and in the first and the third it is in the form of a short stalked cup. The eggs are unknown in *M. sciaenae* Goto, 1894, from *Nivea schlegelii* — 80%, and re-examined by Yamaguti (1958, liii : 80) recording 87 to 97.5% "asymmetry" In these sciaenid spp. the genital atrium includes muscular bulbs and at least 2 kinds of spines, one set slender and slightly wavy, but there are marked differences in the vaginae. In *M. scorpis* Sandars, 1944, from *Scorpis aequipinnis* the "asymmetry" is 59%, and even more pronounced in *Gonoplasius carangis* Sandars, 1944, from *Caranx georgianus* — 50%.

The asymmetry in *M. seriolae* Yamaguti, 1940, is accompanied by the clamp-rows being adherent to the body proper and by peculiar union of the vaginae, and it has been removed to Heteraxininae: *Zeuxapta* Unnithan, 1957 (see below for emendation). *Microcotyle reticulata* Goto, has been similarly transferred to *Dictydenteron* gen. n. (see below) ; but *Prosomicrocotyla gotoi* (Yamaguti, 1934) Yamaguti 1958, (liii: 83), and *P. chiri* (Goto, 1894) Yamaguti, 1958, are retained in Microcotylidae owing to their equal clamp-frills being quite separate in the adult, on either side of the body proper : the complete ontogeny has been studied in the genotype by Bychowsky (1957: 210, figs. 125, 248-256). The partition of the genus *Microcotyle, sensu lato,* as attempted by Tripathi (1956: 239), while being a useful analysis, is perhaps too arbitrary to be adopted without considerable modification.

AXINIDAE Unnithan (1957 : 41) — Microcotyloidea in which the asymmetry of the haptoral region is associated with inhibitions imposed differentially on at least three of the growth-axes: the right and left longitudinal replication axes, and the median body/haptor axis. The clamps themselves show very little modification from the microcotylid type: there may be a fibrous thickening of the capsule wall but secondary cuticularizations are absent (no ribs), but an appendix on the dorsal end of the median spring may be present as in some Microcotylidae. The armature is variously developed on the genital terminalia, and a true cirrus is not developed, only a protrusible penis. There are three subfamilies distinguished by different patterns of this secondary inhibition in the growth-axes of the hind-body.

AXININAE Monticelli 1903, *sensu* Unnithan, 1957: with 7 genera—*Axine* Abildgaard, 1794, *Axinoides* Yamaguti, 1938, *Chlamydaxine* Unnithan, 1957, *Loxura* Unnithan, 1957, *Loxuroides* Price, 1962 *emend, Oligapta* Unnithan, 1957, and *Indocotyle* Tripathi, 1959 (Text-fig. 1A-C).

HETERAXININAE Unnithan, 1957: with 6 genera — *Heteraxine* Yamaguti, 1938, *Gonoplasius* Sandars, 1944, *Zeuxapta* Unnithan, 1957, *Axinoa* gen. n., *Kannaphallus* Unnithan, 1957 and *Heteraxinoides* Yamaguti, 1963.

MONAXININAE Unnithan, 1957: with 7 genera—*Monaxine* Unnithan, 1957, *Crotalaxine* Unnithan, 1957, *Neoaxine* Price, 1945 (=*Amonaxine*

Unnithan, 1957), *Uraxine* Unnithan, 1957, *Allopseudaxine* Yamaguti, 1943 (Text-fig. 2B, 3C-D), *Monaxinoides* Yamaguti, 1963 and *Leuresthicola* Price, 1962. Yamaguti (1963) proposes 3 more subfamilies which are based on characters different from those used in the present rationale.

AXININAE Monticelli 1903—Axinidae in which there is a total inhibition imposed on the median axis of the haptor, while its lateral replication axes are rarely affected, though secondary stimulation is exceptionally absent (*Oligapta* and *Indocotyle*), and the two co-linear rows consist of only the 4 pairs of primary clamps. This absolute inhibition of the median axis affects to some extent the lateral growth of one side of the body at the hind end: the result is that the body is obliquely truncated at a sharp angle and the morphological posterior end faces to one side, edged with a straight row of clamps; near the middle, dorsally, is the intact protohaptor with the persistent larval anchors, and ventrally to it is the combined right and left formative zone for replication of clamps, from which new clamps move slightly distally to take their place in the co-linear rows, their older fellows being pushed laterally so that the oldest clamps are at the outer ends of the rows. The rows are seldom precisely equal, replication being faster on one side than on the other. In Axininae the distal part of the ovary is ascending; the vagina is always single, and in a separate pocket near the 'vulva' there is always a peg-like structure (penis dilator?) with its own muscles. The eggs have filaments at both poles except in *Oligapta*, which has no filaments. The protohaptor with typically two pairs of larval anchors is invariably retained by the adults. Type genus: *Axine* Abildgaard.

Axininae is a remarkably homogeneous group: all of the 17 valid species, except one, occur on Belonidae or Exocoetidae. The well developed vaginal apparatus is unique, and correlated with the lack of strong musculature subservient to protrusion of the male terminalia, and though the latter are often elaborately armoured, there is a truly muscular penis only in *Axinoides*, and doubtfully in *Indocotyle* but in the closely related genus *Oligapta*, and also in *Axine*, the genital atrium has a very characteristic structure: there is a pair of lateral comb-like crescents, a single or double circle of prong-like spines on a muscular ring round the aperture, and the end of the vas deferens carries another crown of spines. When in repose the latter is simply far behind the atrium near the base of a thin roomy sac which is surrounded by masses of prostatic cells, some of which are large with chromophobic cytoplasm and a central nucleus, like the loosely scattered cells round the 'vulva', others are in bunches and more typically "prostatic" (chromophile) the former I would call "hydraulic" cells.

Hydraulic cells are present in all genera I have examined, and particularly well developed in *Loxura* and *Loxuroides*. The atrium is normally much wider than the diameter of the resting penis, and the diameter of the vulval region of the vagina is correspondingly very large, suggesting that the hydraulic turgor of the male duct is explosively destroyed by the ram-like action of the vaginal peg. At the side of the peg-sac in several forms there is a blind pocket leading distally from the vaginal canal proper (both Yamaguti and Hargis have remarked on this problematic duct or sac), and I think that it is obviously to take the pressure-jet at the time of copulation. A similar device is found in the spermathaecae in *Argulus,* and even in other monogeneans; it is an internal safety-valve. Numerous similar "hydraulic-cells" surround the vaginal region in all the Axininae. Another parallel hydraulic or "water-vascular-system" is also developed in this family, (and in others with relatively weak clamp musculature, and also correlated with rapidly swimming hosts, e.g. Opisthogyninae on *Sphyraena* spp.) but this haptoral system has already been referred to in appropriate place by Unnithan (1957). To increase the very necessary firm hold on the gills of these leaping and flying fishes, the delicate clamps are permitted to get a more extensive grip on the filaments by the ventral jaw-rami being hinged near their outer angles: in *Axinoides* both jaws may be hinged in this way, and sometimes two hinges are formed in one ramus.

Axine Abildgaard — Axininae with a marginal vagina and a 3-partite armature of the atrium masculinum and single penis-crown; the vulva often contains a cuticularized plaque against which the peg can operate when the male organ is in place. The long co-linear rows of clamps act as a rule as a single row.

Except perhaps in *A. inada,* where the arrangement is like that in *Heteraxine,* but it is retained in this genus on account of the highly typical genital terminalia, and the ascending ovary, a decision neither supported by its Carangid host nor by the single-filamented egg. In Axininae where the clamps are co-linear and are similarly orientated throughout, it was unfortunate that Llewellyn (1956 *a*: 125) made an ambiguous statement which might imply that Sproston (1946: 452) found them right and left mirror-images in the two rows: there is no need to expect this as a corollary of shortened median haptor axis (shortened to extinction); the two halves of the row are morphologically right and left of course, but the colinear posture being imposed at an early age would affect the shape of even the primary clamps, or at least the later formed pairs on the larval haptor: the early influence on all four pairs of primary clamps is striking in *Oligapta* and *Indocotyle* (Text-fig. 1A). The 7 species of *Axine* considered valid are:—

A. belones Abildgaard, 1794 (Genotype) on *Belone belone* (L.); and from *B. belone euxini* (Günther). Strelkov (1953) obtained his material for ontogenetic studies (see also in Bychowsky, 1957 : 214, figs. 257-260, who also reports that according to Palombi there are other hosts belonging to related genera, but I have not examined the evidence).

A. cypseluri (Meserve, 1938) Price, 1945, on *Cypselurus callopterus* from Galapagos, and on *C. agoo* from Japan (Syn. *A. japonicum* Price, 1945).

A. yamagutii (Meserve, 1938) Price, 1945, on a flying fish off Pacific coast of Mexico.

A. parawa Unnithan, 1957, on *Cypselurus bahiensis* (Ranz.) from Trivandrum, S. India.

A. hemirhamphae Unnithan, 1957, *orthog. emend.* (Syn. *A. hemiramphae* Unn., 1957: non *Axine hemirhamphae* Tripathi, 1959 on *Hemirhamphus xanthopterus* Val., from Trivandrum: distinguished by the haptor being tilted only at about 45° to the body-axis, and only slightly wider than the rather evenly wide body, in contrast to the fore-going spp. in which the haptor besides being about twice the width of the body, is tilted nearly parallel.

A. tripathii (Tripathi, 1959) Yamaguti 1963 pro *A. hemirhamphae* Tripathi, 1959 (homonym but not synonym of *A. hemirhamphae* Unnithan, 1957, on *Hemirhamphus georgii* Val. from the Hooghly River, W. Bengal, and Puri, Orissa, Bay of Bengal: distinguished, *inter alia,* by the haptor being at right angles to the body-axis but stretching away to one side, causing the whole animal to be 'L'-shaped, and its length 4½ times the body-width — the latter is the more important since the former may be a transient posture; an unusual character is the single row of relatively very large testes.

A. inada, Ishii & Sawarda, 1938, on the Caraangid *Seriola quinquiradiata* from Japan: exceptional in the asymmetrical clamp-rows, the shorter being only 6% of the longer, and the egg having a single polar filament (characteristic of *Heteraxine* spp., but the vagina and atrium are like those of *A. belones:* a transitional species of special interest).

Axinoides Yamaguti, 1938 emend.—Axininae in which the clamps do not have an appendix on the dorsal end of the median spring, but in which the ventral, at least, of the jaw-rami are jointed near their mid-length; vaginal apparatus as in *Axine,* but never marginal (dorsal, median or laterally placed); atrium masculinum never armed. Genotype: *Axinoides tylosuri* Yamaguti, 1938, on *Tylosurus schismatorhynchus* from Japan. 4 other species considered valid: —

Axinoides gracilis (Linton, 1940) Sproston, 1946 on *Tylosurus marinus* (Walb.) from W. Atlantic at Woods Hole and Florida: recently rediscovered by Hargis (1956:xi: 155), he confirms the protohaptor and on the basis of the very variable position of the vagina from mid-dorsal to nearly supramarginal, he emends the generic diagnosis.

A. raphidoma Hargis, 1956 on *Tylosurus raphidoma* (Ranz.) from Florida: Hargis (xi: fig. 1) shows the anchors (protohaptor) as we find them in other species, on the dorsal side, the clamps are fewer than usual: 5+12 on the left (posterior lobe) and right respectively; the crown of a muscular penis is shown reduced to cuticularized papillae; vagina obliquely median-dorsal; crura not confluent.

A. kola Unnithan, 1957 on *Athlennes hians* (Val.), from Trivandrum, S. W. India: vagina median with cuticularized papillae in funnel much longer than in the genotype; muscular penis with ejaculatory bulb also similar, but clamps (25-27+37-41) are enclosed in hardened fibrous capsules which are jointed laterally and posteriorly, like the ventral jaw-rami but not opposite to these hinges, and the anteriormost clamps are longer with long reflected ventral jaw-rami; the intestinal crura are confluent.

A. sebastisci Yamaguti, 1958, from *Sebastiscus marmoratus* from Japan: there is a constriction at the base of the very narrow neck opposite to the mid-dorsal vagina; the 38-42 clamps are described but not figured in detail, nor are anchors mentioned.

Species incertae sedis: Axine resplendens Caballero, Bravo & Grocott, 1954, on *Tylosurus fodiator* from Eastern Pacific: according to the remarks of Hargis it may belong here, but I have not yet seen this paper.

Chlamydaxine Unnithan, 1957 emend.—*Axininae* unique in having a metahaptor, developed on one side only, growing laterally then anteriorly on the ventral side; body flattened to a broad triangle and cuticle with transverse rows of delicate papillae; vaginal apparatus with a well developed peg and caecum, vaginal duct thick walled and with cuticularized lining, all marginal at level of atrium: penis not strongly muscular with a minute head of papillae; intestinal crura confluent, a few branches entering the metahaptor. Monotypic with *C. truncata* (Hargis, 1956) Unnithan, 1957, *orthogr. emend.*

Hargis placed this species in *Axinoides* but it is excluded by the thickened papillose cuticle, the marginal vagina, and the clamp jaw-rami being unjointed laterally, but predominantly by the unique unilateral metahaptor. On the gills of *Tylosurus raphidoma* (Ranz.) from Florida, S.E. USA. (Text-fig. 2A).

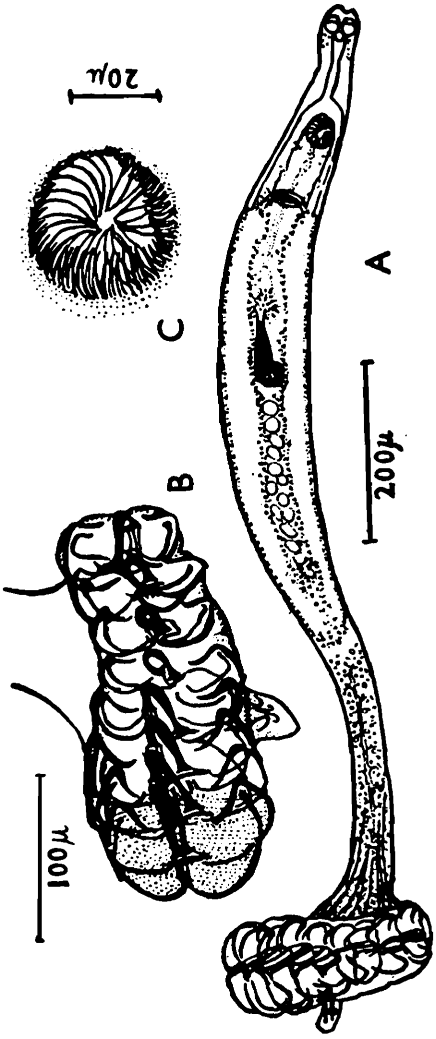
Loxura Unnithan, 1957, *s. str. emend.* Monotypic with *L. ananaphallus* Unnithan, 1957, on *Tylosurus leiurus* (Blkr.) from Mandapam, S. India: Generic characters related to *Axinoides*: dorsal vagina in the lateral field but not marginal, numerous hydraulic cells surround the vulva, peg slender, no receptaculum seminis, but wide canal apparently distensible; unique pine-apple like penis beset with close-packed pointed spines with notched bases, musculature weak for this huge organ (occupying a larger field than the ovary) but surrounded by a sheath of prostatic cells extending from the atrium to mid-body (thought to be hydraulic in function); atrium unarmed but apparently extensive surrounding the penis and opening in a muscular ring with a dentate soft internal rim; testicular zone remarkably short, only about half the body-width in length, testes in double row; crura end bluntly well above haptor, which has a clear "water-vascular canal" in two arms from a median stem. Haptor margin in two wide curves projecting beyond the body at each side, numbers of clamps practically equal; clamps increase in size medially; very slender sclerites, only ventral jaw-rami jointed, no spring-appendix, about twice as wide as long, capsule not thickened, but finely fibrous. Only one pair of rather large anchors found; egg with two short thick filaments.

Loxuroides Price, 1962, *emend.*, for *Loxura sasikala* Unnithan (1957 p. 105, figs. 11 a-m) on *Cypselurus oligolepis* (Blkr.), from Mandapam, S. India. Generic criteria now seen to be quite distinct from *Loxura*: *unlike* the last 3 genera, the genital atrium has a characteristic armature, not in 3 parts as in *Axine*, but a single diadem-like open circlet of highly muscular or other radial fibres as a thick rim holding a double row of peculiar broad spines with curved tips : radial extrinsic muscles could apparently pull open the ring to admit the emergence of a swollen penis head, which in repose lies at the base of this roomy atrium, its head of spines, like a sun-flower bud when not erected, are dagger-shaped on broad imbedded bases set on the intrinsic muscles of the head: extrinsic muscles absent and correlated with the hydraulic cells surrounding the atrium ; vesicula seminalis large proximal ; vaginal apparatus in the same relative lateral position as in *Loxura,* well behind the atrium ; the peg is a broad cone with notched tip, there is a large cuticular pad, the vaginal field is very wide and surrounded by hydraulic cells—a field of comparable size to that of the atrium masculinum ; a large receptaculum seminis is developed half way down the vaginal canal which opens independently into the ootype. In contrast to *Loxura,* the testicular field in *Loxuroides sasikala* occupies at least half the body-length, the more numerous follicles being in about 4 rows. The haptor-margin is nearly parallel with the body-axis, it is not in two curves, but it has a similar "water-vascular system" Right and left clamp rows are nearly equal, but only the "posterior" row projects beyond the body-edge and the crus of this side is much longer. The clamps are longer than wide, both jaw-rami are hinged and the ventral is the shorter jaw, there may be an appendix on the end of the spring. Both pairs of larval anchors slender with long roots.

Oligapta Unnithan, 1957 — Monotypic with *O. oligapta* Unnithan, 1957 on *Hemirhamphus georgii* (Val.) from Mandapam, S. India. This curious species was the first of its kind to be described : at first sight not Microcotyloidea., because there are only 4 pairs of clamps, but they are co-linear and are orientated in the same direction, and separated by two pairs of anchors, and there is a marginal vaginal apparatus as well as a tri-partite hook-bearing apparatus in the genital atrium — all characters of *Axine* Abildgaard. The second of this kind of Microcotyloid was in fact discovered over two years previously but not published till later, by Tripathi (1959), curiously on the same host-species, but from the opposite corner of India. Being unaware of *Oligapta* when going to Press, he created a new subfamily for it in Discocotylidae, a pardonable error since the typical axinid vaginal peg was not found. The numerous differences are instructive and will be noted below. In *Oligapta oligapta* the whole internal organization is precisely that of *Axine*: there is one unique feature of the genital system: the median vitelline canal gives off an accessory branch to the intestine of the right side (the normal vitello-intestinal canal passes into the same crus straight from the ootype-oviduct junction as usual) and also, the eggs are without polar filaments. The clamp-spring lacks an appendix but the ventral jaw-rami are jointed the proximal anterior shoulder-wings of the latter have a wide flange of muscle fibres and the whole of these large clamps is enclosed in a thick fibrous capsule. The absence of any secondary replication of the clamps is an interesting exception in Microcotyloidea and alone is sufficient to separate the genus from *Axine.*

Indocotyle Tripathi, 1959, Monotypic with *I. hemirhamphae* Tripathi, 1959, on *Hemirhamphus georgii* (Val.), from the Bay of

Bengal at Puri, Orissa, and from the River Hooghly, Calcutta region, India. The lack of detail in the description and figures have been remedied by the kind loan of original material (Text-fig. 1A-C). The filiform body is more than one-third haptoral peduncle, and one-quarter is "neck" (in extended specimens). Clamps are in a graded row, obliquely to nearly perpendicular to the body/stem axis, the more posterior clamps are the larger in the living attitude, but the morphologically posterior clamps are of course, in the middle of the co-linear row; a small protohaptor projects from the dorsal posterior margin between the middle pair, bearing two pairs of anchors with sharply recurved points at least half as long as their shafts (the roots are partly hidden by the clamps in the present material). The clamps are extremely delicate, though the haptor is stout, and they appear sessile; the ventral end of the spring-loop has a narrow horizontal accessory piece suspended by a lightly cuticularized membrane which extends laterally to connect with the distal tips of the ventral jaw-rami — these are articulated at about half their length; the dorsal arm of the median spring is short but connected with a double rib-like cuticularized support to the distal edge of the dorsal capsule wall making a tenuous



TEXT-FIG. 1. *Indocotyle hemirhamphi* Tripathi, 1959. A. Whole animal, ventral view; B. Haptor with 8 clamps and posterior-dorsal proto-haptor with anchors, ventral view; C. Genital corona, ventral view (Original, from specimen on loan from Dr. Y. R. Tripathi).

connection with the dorsal jaw-rami, which are in a single piece. The haptoral peduncle is packed with small gland-cells draining into a median duct, but distally it becomes confused by a dense granular mass of different glandular tissue. The ends of the intestinal crura were hidden in the vitelline mass. The lips of the vagina are broad and cuticularized, but just within, the vulva is finely corrugated, apparently hardened but stains differently: there are two lateral ducts which become obscured in the lateral vitellaria. There is a double circle of genital hooks: the outer, probably belong to the atrium and are extremely fine (about 48 of them) projecting ventrally, the inner (about 14) are much wider, and in repose point inwards and dorsally, probably attached to the tip of the penis. No eggs were observed in any specimen. (Text-figs. 1A-C).

HETERAXININAE Unnithan (1957), *emend.*—Axinidae in which the differential inhibition on secondary haptoral growth is most strongly imposed on the lateral clamp rows, though there is always some inhibitory influence on the growth of the body/haptor axis, so that the clamp-rows are more or less adherent to the sides of the body, and their unequal length results in a lateral torque (in the habitual posture of the worm along a gill-filament, *vis-a-vis* the more or less oblique posterior-anterior streaming of the cibo-respiratory current of the fish) so that the body-axis is inclined towards the shorter line of fixation.

As the short row approaches extinction (in *H. karavoli* and *Axinoa*) the body appears to "stand on" the long row (tilted over to nearly 90°), but the lateral nature of this now posterior haptor is seen in the intestinal crus following it to its morphological posterior end at the origin of the short side: the anchored protohaptor is always lost in the adults of Heteraxininae. As a result of this torque imposed from very early life, the whole of the gonad field tends to be curved with the convex side towards the long row (as in *H. heterocerca*). This is in marked contrast to Axininae where the gonad-field and body are straight: because from early life the clamp rows have been added practically two by two on either side of the median axis of the body, albeit in a straight line, and the torque has been applied very gradually as the body-axis bends nearly parallel to its straight haptor. In Axininae the level of tilting is *behind* the gonad-zone, so the alignment and symmetry is not affected at all, whereas in Heteraxininae where the clamp-rows are free to grow up the sides of the body, the longer row holds the hinder half of the gonad-zone and crural branches of that side, while the rest is tilted away with the bending body: the level of tilting being *within* the testicular zone. The degree of asymmetry, as in Gastrocotylinae, depending on the length of gonad-zone embraced by the clamp-row(s), and on their *inequality*. In *Zeuxapta* and *Dictydenteron* the right and left clamp-rows are not very different in length (in spite of the differences in numbers of clamp-units in the latter), and what is more important, they have been built up on wide flanges which allow of some independent movement of the body, though the latter is restricted by the nearly equal "pull" from each side of its hind end: in fact as published figures show, the level of flexing is even higher up the gonad-zone—at its *anterior* limit in these genera and in *H. oligoplitis*, but behind the gonad-zone in *Kannaphallus* and *Axinoa,* which accounts for the lack of somatic involvement in their postural tilting, except for the intestinal branches which always point to the origin of the clamp-rows : more or less medially in direct extension of the body-axis in Axininae and also in Heteraxininae, where the rows are sub-equal ("V" — Shaped), and laterally in Heteraxininae in which there is a marked differential inhibition in the clamp-rows. No metahaptor is ever developed.

In Heteraxininae the distal end of the ovary is descending as in Microcotylidae, to which they are in many respects related: transitional genera being *Gonoplasius* and *Zeuxapta*. The eggs usually have a fine filament at the anopercular pole only. The vaginal apparatus is various but never with a peg, and the male terminalia muscular, but never an eversible cirrus ; the spination of the atrium is various but never axinid, and may be absent. The clamps are sometimes in graded sizes in the longer row, or in uniformly different sizes in the two rows, but they are not adaptively remodelled from the microcotylid pattern, nor are the jaw-rami broken by hinges, but an appendix often occurs on the end of the spring (Text-fig. 3A). The 5 genera are distinguished by internal characters, and *Heteraxine* Yamaguti, the type genus, may be composite ; *Axinoa* is perhaps transitory from Axininae, and of uncertain position, its hosts being beloniform fishes whereas the others are from Carangidae, Serranidae, and Sciaenidae.

HETERAXINE Yamaguti, 1938, *emend.*—Heteraxininae in which the number of clamps in the inhibited row are usually less than 40% (exceptionally about 62%) of the longer row and the length of the shorter less than 20% (exceptionally about 60%). The vagina is unarmed mid-dorsal. Genotype: *H. heterocerca* (Goto, 1894) on *Seriola quinqueradiata* (=*S. aureovittata* T. & S.) from Japan.

Other species are: *H. seriolae* (Ishii, 1936) Yamaguti, 1938 on *Seriola aureovittata* T. & S., from Japan: (Text-figs. 2C, 3A) clamp-rows length of the shorter (also with about 9-10 clamps) 17%, numerically 36-39% ; testes over 50? ; vaginal structure identical with last ; eggs 149-166 μ long, one filament.

H. carangis (MacCallum, 1918) Yamaguti, 1938 on *Caranx hippos* (L.), from U.S.A., E. Coast : clamps in short row 19 (28% of longer) ; atrium with two lateral spine-rows and penis spiny ; mid-dorsal vagina encircled by spines ; testes 40-50 ; egg with 2 filaments.

H. scomberomori Koratha, 1955 is known to have a spiny vagina, but otherwise this species is insufficiently documented.

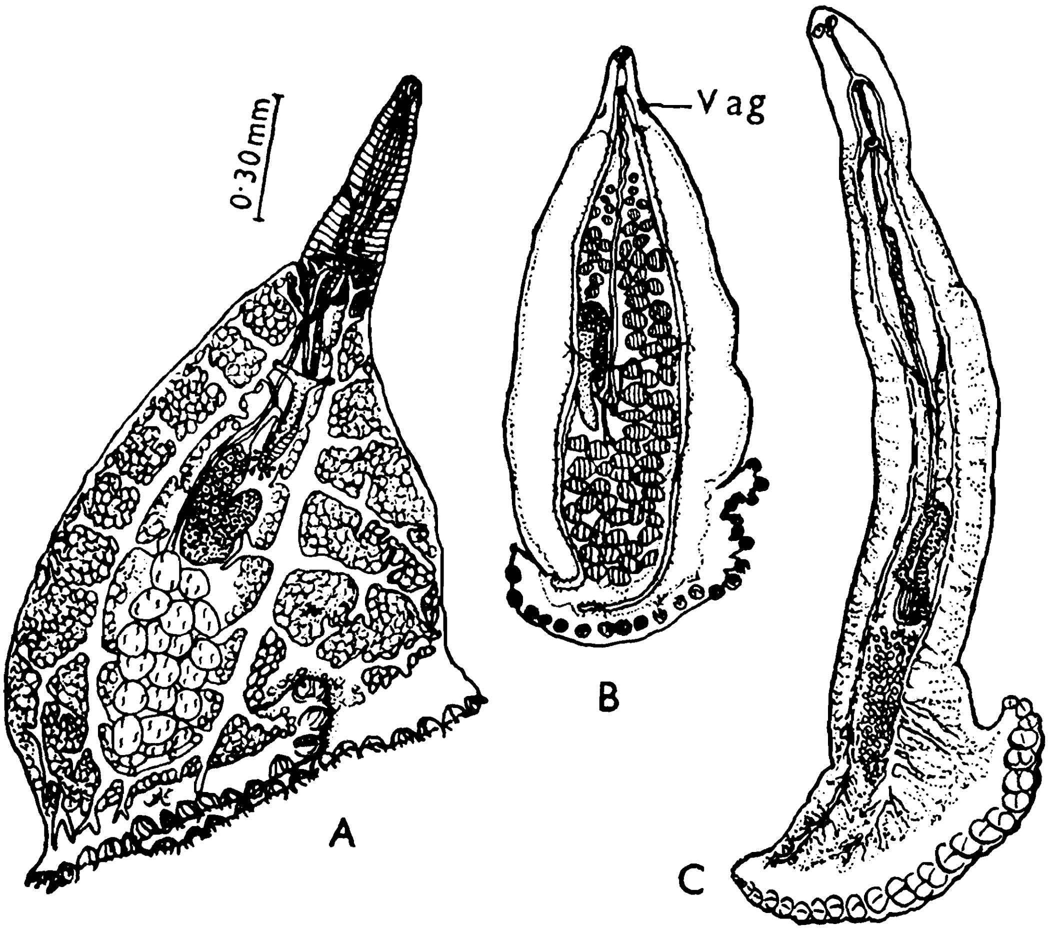
H. karavoli Unnithan, 1957 on *Formio niger* (Bloch) from Trivandrum, S. W. India : again only 6 small clamps in short row ; but widely spaced, so that both by length and number the short row is *ca* 12% of longer ; atrium and penis highly muscular with small comb-like spines and 3 large imbedded, rhabdite-like, spicules ; unarmed vagina a single duct, leading direct to ootype.

H. mcintoshi (Price, 1962) Yamaguti, 1963 syn. *Allencotyla mcintoshi* Price, 1962 on *Seriola lalandii* from Florida, U.S.A. ; vagina median dorsal.

Heteraxinoides Yamaguti, 1963, *emend.* — Heteraxininae resembling *Heteraxine* except that the vagina is absent or unknown (?). Genotype: *H. triangularis* (Goto, 1894) Yamaguti, 1963 syn. *Axine triangularis, Heteraxine triangularis* Yamaguti, 1938 on the serranid *Anthias schlegelli* Günther, from Japan: only 6 clamps on short side (both by numbers and length about 17%); cup-like atrium lined with conical spines; vagina? ; testes about 12 ; egg ?

Other species are:

H. chinensis (Yamaguti, 1937) Yamaguti 1938 on the pomadasyid *Hapalogenys nitens* Rich. from Japan: also 6 similar clamps on short side (*ca* 17%); atrium with large spines laterally and 2 arcs of smaller spines ; vagina absent ; eggs ? ; testes 12.



TEXT-FIG. 2. A. *Chlamydaxine truncata* (Hargis, 1956) Unnithan, 1957—whole animal, ventral view (from Hargis, 1956); B. *Allopseudaxine katsuwonis* (Ishii, 1936) Yamaguti, 1943—whole animal, dorsal view (from Ishii, 1936); C. *Heteraxine seriolae* (Ishii, 1936) Yamaguti, 1938—whole animal, ventral view (from Ishii, 1936).

H. oligoplitis (Meserve, 1938) Hargis, 1956 (Syn. *Axinoides oligoplitis* of Sproston, 1946 ; *H. oligoplitis* of Hargis (1956, xi: 160), and *H. oligoplites* of Bychowsky (1957: 253), on *Oligoplites saurus* (Bl. & Sch.) from Equador ; clamp-rows 52% in length ratio and numerically 40-43% (16-18 in short row) ; atrium with double lateral rows of spines ; vagina ? ; testes 28-39 ; eggs ?

H. xanthophilus Hargis, 1956, (*incertae sedis ?*), on the sciaenid *Leiostomus xanthurus* Lacep. (Syn. *H. xanthophilis* Hargis (1956, xi, 160, in description but the former spelling on p. 157): clamps in short row 18-21 (62%), and the relative length of row 63.5% ; atrium with two lateral spine-bearing pads and 2 kinds of spines ; egg with a single filament ; vagina unknown.

H. xanthophiloides Price, 1962, on *Leiostomus xanthurus* from U.S.A. (Massachusetts). 4.4 x 9.55 mm ; 36 clamps on longer row, 20 on shorter row.

Kannaphallus Unnithan, 1957. Genotype: *K. virilis* Unnithan, 1957, on *Caranx atropus* (Günth.) from Trivandrum, S. W. India: haptor similar to *Heteraxine* spp., with 12-15 clamps in short row of similar size and about 30% of long row, which embraces only about the last fifth of the testicular field and is tilted only about 45° ; the clamps are nearly square, and there is an appendix on the spring; numerous scattered head-organs, but the intestinal lateral branches are unique: very regularly increasing in length, without tertiary branches, and the long posterior branches are nearly parallel pointing towards the long clamp-row, the crus of the long side extending as far as the 4th primary clamp where the vitelline fields are confluent (as in *Axinoa* and *Heteraxine* spp.). In other *Discocotylinea* the crural branches are not flexed backwards regularly but are given off more or less perpendicularly and then ramify irregularly. Testes more than 100, and there is a unique *penis-gun* consisting of a long cuticularized tube, a basal ejaculatory bulb, and a large muscular compressor distally derived from the atrium. There are *two dorsal vaginal pores* with muscular bulbs the two ducts eventually opening into the vitelline ducts. The ovary is double-arched as in *Heteraxine,* but the eggs have a filament at each pole.

Zeuxapta Unnithan, 1957: created for two potential homonym spp. of *Heteraxine seriolae* Ishii, having a unique vaginal apparatus: two dorsal vaginae at opposite ends of a transverse vulva which opens in a median unarmed pore ; the gonads are crowded into the posterior quarter of the body proper and are embraced on one margin by an extensive clamp-frill, on the other side of the only slightly tilted hind end is a clamp row of only half the length, barely reaching the gonad-zone, the nearly equal sized clamps are *twice as crowded* in the latter row. Genotype: *Z. zyxivaginata Unnithan,* (1957: 43) Syn. *Microcotyle seriolae* Yamaguti, 1940, nec. *Axine seriolae* Ishii, 1936 (=*Heteraxine* s.), nec *Axine seriolae* Meserve, 1938 (=*Heteraxine meservei* Sproston, 1946 — renaming of homonym), on *Seriola aureovittata* from Japan: clamps of short crowded row 87-90% of longer but only half as long, clamps of *graded* sizes, the largest being thrice the smallest ; genital atrium wide, with extrinsic muscle-fibres, but unarmed ; eggs 105-132 μ long with a single very fine, long, filament.

Z. meservei (Sproston, 1946) comb. n., (Syn. *Axine seriolae* Meserve, 1938, non *Axine seriolae* Ishii, 1936 ; *Heteraxine meservei* Sproston, 1946, a renaming of the homonym) — the wording of the re-assignment of genus for these species in Unnithan (1957, p. 43), is ambiguous, so that greater clarity has been attempted in this place. I do not consider that Meserve's species is certainly identical with Yamaguti's, which is selected as the genotype because there is a clearer figure of it. In both, the transverse vaginal commissure, or 'vulva', with its median pore is between the upper end of the vitelline fields and a marked bilateral constriction in the fore-body, and is as far behind the genital atrium as the latter is behind the intestinal bifurcation. The atrium is unarmed but in *Z. meservei* the whole of the intercrural field from the brain to the ovary, on the ventral side, is covered with minute spines ("sharply recurved hooks", "several hundreds closely set") — a feature scarcely likely to have been overlooked by Yamaguti. The length of the clamp-rows is again in the ratio of 50%, but there is no graduation in size, according to Meserve they have a size-range of not more than 10%, but on one side they are more crowded, as before, the numerical ratio being 71-72.5% ; similar eggs, 96-136μ long, with a fine filament one and a half times as long, at one pole. Host: *Seriola dorsalis* (Gill) from the Galapagos Islands.

Gonoplasius Sandars, 1944 — removed from Microcotylidae owing to its markedly asymmetrical haptor which, however is sharply demarcated from the body (one-sixth its length): like *Zeuxapta,* this is a transitory genus of doubtful affinity, but the double (paired) 'vulvae' suggest possible affinity with the latter; the spine complex of the genital atrium and spined penis bear some resemblance to the condition in some Heteraxine spp. rather than to microcotylids (other than the *M. heteracantha* — group which have a far more highly differentiated complex of muscular loculi and 3 or 4 kinds of spines). *G. carangis* Sandars, 1944, the type species, from *Caranx georgianus* from W. Australia : a slender worm, less than one-tenth as wide as long, with only 17 clamps on one side and 34 on the other, the anterior being smaller than the middle clamps ; which taken with the relative secondary inhibition of the one row, provides its link with *Heteraxine.* The original diagnostic character is the conspicuous head-glands: paired semi-lunar groups and a median preoral group, but such occur frequently in *Microcotyle, sensu lato,* and are of generic importance only in combination with other criteria. The genital atrium has lateral muscle-pads bearing 5 small and 5 much longer spines, and the penis has 5 small spines on its muscular tip. Two spiny suckers, probably associated with dorsal 'vulvae' and a voluminous median vaginal duct appear to be characteristic.

Other species: *G. longirostri* (Robinson, 1961) Price, 1962, syn. *Microcotyle longirostri* Robinson, on *Longirostrum platessa ;* from New Zealand.

Axinoa gen. n. : erected for *Axine aberrans* Goto, 1894 (Genotype) apparently representing all-but-complete inhibition of one of the clamp-rows ; the single clamp interpreted as the remnant of the inhibited row ; analogous to the two derelict clamps in the gastrocotylid *Engrauliscobina thrissocles* (Tripathi, 1959) gen. n. (The Greek suffix *'oa',* the firnge of a garment, added to the stem of *'Axine'* forms the name of this transitional genus): the main clamp-row has become posterior and in front of it are the intestinal branches of the uninhibited side and the vitellaria corresponding are confluent with the opposite side as in *Heteraxine ;* vagina single mid-dorsal, spiny within ; genital atrium armed with conical spines, and penis with a corona of spines. The spiny atrium excludes *Axinoa* spp. from *Axinoides* as emended by Hargis, and Unnithan.

Axinoa aberrans (Goto, 1894) comb. n. (Syn. *Axine a.*, Goto; *Axinoides a.* of Price, 1945, and others), on *Tylosurus schismatorhynchus* (Blkr.) from Japan 25-40+one clamps; 16-25 testes; eggs unknown.

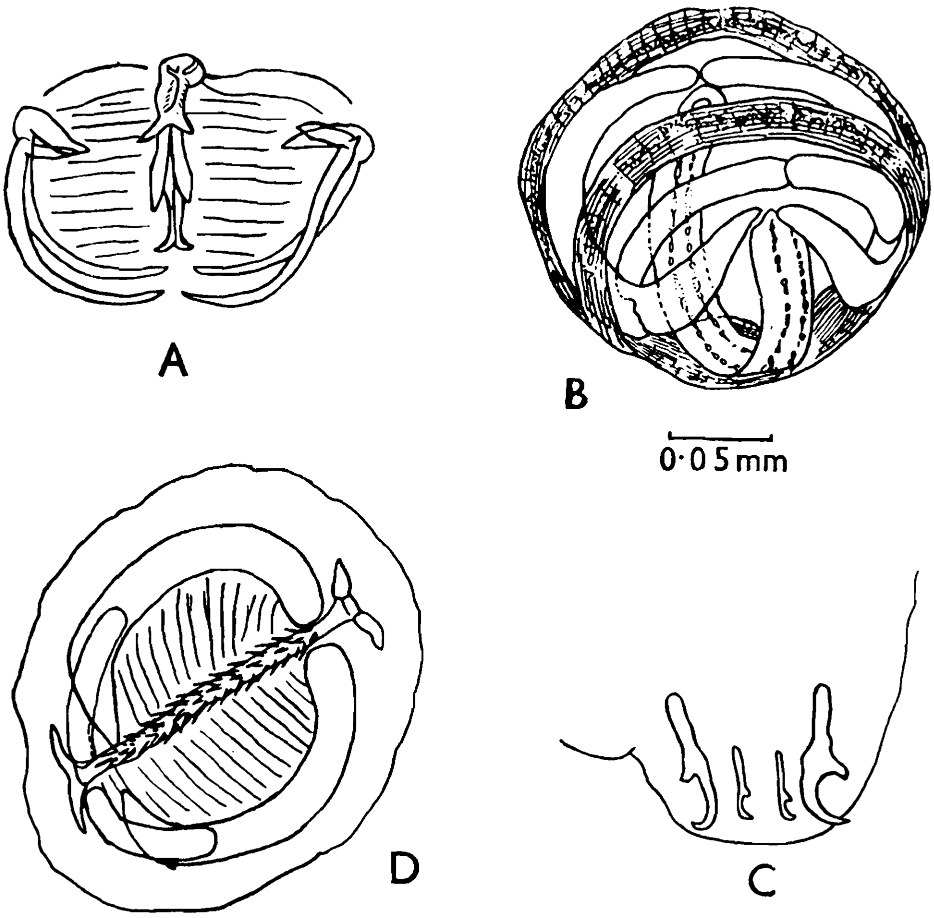
Axinoa meservei (Price, 1945) comb. n. — (Syn. *Axine aberrans* of Meserve, 1938: renamed by Price without publication of reasons due to insufficient information) on *Tylosurus fodiator* Jord. & Gilb., from American Pacific off Columbia. In Meserve's fig. 59, there are 1+41 clamps, and about 96 testes; a single duct leads from the ampoule-like vagina to meet the transverse vitelline duct of the left side: no other details shown for the contracted specimen drawn. The validity of the species must remain *sub judice,* though the testes are 4 times more numerous than in the genotype.

MONAXININAE Unnithan, 1957 *emend*—Axinidae in which there is complete inhibition of one side of the haptor (but not of the haptor/body axis of that side in all genera), the clamps when less than 50 in the single row show a graded diminution in size proximally, and in the genera on Thunnidae they have greatly thickened and simplified sclerites acting as supports for a cupuliform sucker of a characteristic type (Text-fig. 3B). The distal part of the ovary descends in all genera, but the vagina is mid-dorsal in those parasitic on Belonidae and *Formio,* and paired lateral in those on Thunnidae; male terminalia armed or not; eggs with two polar filaments. Protophaptor retained in adults by those on Thunnidae. Hydraulic system in haptor of all.

MONAXINE Unnithan 1957, *emend.* Genotype: *Monaxine formionis* Unnithan, 1957, on *Formio niger* (Bloch), from Trivandrum, S. W. India. The complete inhibition of the one side of the haptor has included inhibition of growth of the body/haptor axis, so that unlike *Heteraxine* spp., there is no "toe-of-boot" — like projection of the haptor on that side, but on the other side the body/haptor axis has a correspondingly greater development than in *Heteraxine*; a triangular wing of the body carrying additional branches of the intestinal crus of that side supports the proximally projecting clamp-row of more than 70 similar simple clamps. Median dorsal vagina is unarmed, has a sphincter and a wide surround of chromophilic secretary cells. Muscular rim of atrium masculinum with 2 kinds of spines, coarse papilla-like spines on penis-head. Eggs unknown.

Monaxine bivaginalis Ramalingam., 1961 on *Formio niger* (Bloch). from Mandapam, S. E. India.

NEOAXINE Price, 1945, *emend.* Monotypic with *Neoaxine constricta* (Yamaguti, 1938) Price, 1945 (Syn. *Axine constricta* Yamaguti, 1938; *Amonaxine constricta* Unnithan, 1957 — genus created in ignorance of Price (1945). Recorded only once, on *Tylosurus schismatorhynchus* from Japan. The single clamp-row has 55-58 similar clamps, and its organization appears similar to *Monaxine,* but its main character is a marginal funnel with an incomplete circlet of "pedicellaria-like" spines, but no peg: another character excluding it from Axininae (apart from the inhibition of half the haptor and loss of anchors) is the unarmed atrium containing a penis armed with a well developed head of 50-80 spines. There is a strong constriction at the level of the vagina ; one polar filament of the egg is much shorter than the other.



TEXT-FIG. 3. A. *Heteraxine seriolae*, clamp (from Ishii 1936); B. *Uraxine macrova* Unnithan, 1957—clamp modified as sucker, showing lips of fibrous capsule with gland-cells (from Unnithan, 1957); C. *Allopseudaxine katsuwonis*, protohaptor with two pairs of anchors and D. Clamp modified as sucker in thick capsule (both from Ishii 1936).

CROTALAXINE Unnithan, 1957, *emend.* Monotypic with *Crotalaxine serpentina* Unnithan, 1957, on *Athlennes hians* (Val.), from Mandapam, South India. Haptor a unilateral frill of rather large clamps in fibrous capsules, but not modified other than the dorsal jaw-rami being longer than the ventral, and having a joint just proximally to their curvature, clamp-muscles and hydraulic ducts both conspicuous. The body/haptor axis does not share the inhibition of the clamp-row on that side, but is extended for more than half the length of the clamp-row posteriorly, forming a mobile wing which brings the tilting level of the body obliquely, behind the testicular zone. The 36 clamps in *C. serpentina* show the persistence of slight inhibitory influence in their gradual diminution to half-size proximally. The extreme narrowness of the body permits only a single row of elongated testes. The muscular penis within a fibrous sheath, but no pars prostatica or hydraulic gland-cells developed, and the muscular rim of the atrium is also unarmed. The vagina resembles that in *Axinoides* in being median dorsal and in having a peg, and a radial muscular vulva surrounded by what may be hydraulic cells over a wide area ; the vaginal duct as in *Monaxine* runs directly back to the ootype ; eggs unknown.

URAXINE Unnithan, 1957 *emend.*—Monaxininae, the unilateral haptor held tilted posteriorly between 45° and 90° to the body-axis, the level of tilting behind the testicular zone ; relatively few large clamps tending to become smaller proximally ; distally there is no extension of the body/haptor axis, the crura extending to the base of the laterally projecting protohaptoral lobe bearing its two pairs of larval anchors. Cupuliform sucker-clamps with thick muscular capsules have sticky-glands within their rims (Text-fig. 3B) ; sclerites grossly thickened and simplified, but both rami of both jaws articulated and participating in the sucker framework, moreover the sucker is not of the "open" type (as in Heteromicrocotylinae, Mazocraeidae, Thoracocotylinae, and Choricotylinae) the jaws being still opposable by the action of the wide 3-ribbed spring, decorated by two lines of muscle-emplacements — a "C"-shaped meridian of the cup, but without appendages on its ends. Paired head-organs and the round oral suckers are scarcely half as big as the pharynx: paired vaginal pores as unarmed slits in the dorsal lateral fields in the zone of the crural bifurcation, the vaginal canals form a "Y"-shaped system opening directly into the ootype ; genital atrium with a wide muscular rim set with 17-19 elongated lozenge-shaped spines admitting an unarmed bifid penis ; testes less than 25, mostly par-ovarial and post-ovarial, a few may be pre-ovarial. Large operculate eggs with 2 polar filaments. Parasitic on Thunnidae. Genotype: *Uraxine chura* Unnithan, 1957. Though the shape of these worms is very like that of *Pseudaxine,* the clamps and vaginae are entirely different.

Uraxine chura Unnithan, 1957, on *Euthynnus alleteratus affinis* (Cantor), from Trivandrum, S. W. India. Specific characters include a double row of par-ovarial testes and only 3 or 4 post-and pre-ovarial ; atrial corona of 19 spines ; largest of the 15 clamp-suckers 180 × 100 μ eggs 168 × 62 μ

Uraxine macrova Unnithan, 1957 (Syn. *U. chura macrova* Unnithan, 1957—sub-species now given full species rank), on the same host fish with genotype. Distinguished by most of the testes being post-ovarial and a single par-ovarial row ; atrial corona of 17 spines ; largest of the 15 clamps 210 × 168 μ ; eggs 260 × 92 μ. Both clamp muscles and hydraulic vessels are more strongly developed in the haptor of this species.

ALLOPSEUDAXINE Yamaguti, 1943. Monotypic *A. katsuwonis* Ishii, 1936 (Syn. *Pseudaxine katsuwonis* Ishii, 1936), on *Katsuwonus vagens* (Lesson) from Japan. Genus very close to *Uraxine,* but a much larger type (8.0 mm. compared with about 6 mm.), and over 80 testes which are nearly as numerous pre-ovarially as post and par-ovarially packing the inter-crural field ; genital corona of 12 spines ; the clamp has become an open sucker framed by the opened ventral jaw-rami but supported at one end by the short thick dorsal jaw-rami. The meridional spring is shown straight (optical effect ?), and at each end it carries a bifid appendix. There are indications of transverse muscle-fibres from the spring across the walls of the cup-like capsule, which has an exceedingly thick rim. 24 clamps are shown, the proximal on short stalks ; eggs 216 × 66 μ ; the anchors are 48 and 28 μ long respectively, with relatively longer roots than in *Uraxine* spp., though their total length is similar. There appears to be only the original record for *Allopseudaxine katsuwonis* (Ishii, 1936 : 786-7, figs. 7, 8) Text-figs. 2B, 3C & 4D herein.

HETEROMICROCOTYLIDAE* (Yamaguti, 1963) *S. Str. emend.*

Microcotyloidea *s. str.* in which asymmetry within the haptor suggests a differential stimulation of secondary growth, rather than the differential inhabition, which is characteristics of the family *AXINIDAE.* The growth differences along the axes of the haptor in Heteromicrocotylidae are not only quantitative but, uniquely, qualitative also. Hence, a usually asymmetrical haptor bears clamps of mixed types, but these are mere remodellings on the simple microcotylid pattern, and no additional sclerites appear in the essential structure. The protohaptor (anchor-bearing lobe of the larval haptor) may be lost in the adults, or retained as a distal vestige on the end of the euhaptor (definitive haptor of the adult) incorporating the larval clamps distally. A *metahaptor* may be developed proximally on one or both sides as a continuation of the clamp-rows of the euhaptor, but showing a discontinuity by its own structure (it may be wing or shelf-like, and may be wholly or partially free of the body as a morphologically anterior lobe in relation to the euhaptor), the discontinuity may appear in the form and in the size of its clamps. A similar discontinuity often marks the passage from the primary (larval) clamps to the secondary clamps in the euhaptor, particularly when the latter are atypical. The distal part of the ovary descends ; the vagina opens dorsally in an unarmed pore, but the nature and armature of the male terminalia is highly variable. Parasitic on Carangidae, Stromateidae and Chirocentrus.

The three subfamilies are characterized by the level of incidence of the secondary differential growth stimuli along the haptoral axis :—

HETEROMICROCOTYLINAE subfam. nov.—5 genera: *Heteromicrocotyla* Yamaguti, 1953 ; *Heterapta* Unnithan, 1961 (incl. *"Diplasiocotyle" chorinemi* Tripathi) ; *Dicotyle* Tripathi, 1959 ; *Dictydenteron* gen. nov. ; and *Carangiamata* gen. nov.

CEMOCOTYLINAE subfam. nov.—4 genera: *Cemocotyle* Sproston, 1946 ; *Xureliphilus* gen. n. ; *Tripathiana* gen. n. ; and *Megamicrocotyle* Tripathi, 1956.

PYRAGRAPHORINAE subfam. nov.—2 genera: *Pyragraphorus* Sproston, 1946 ; and *Hargisiella* gen. n.

HETEROMICROCOTYLINAE subfam. nov.—Heteromicrocotylidae, with atypical clamps on one or both of the usually unequal sides of the haptor: these are usually on a euhaptor more or less adherent to the body, or on an adherent bilateral metahaptor (in *Heterapta* only).

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* This family now preoccupied by Yamaguti, 1963 was originally erected in the first draft of this paper and reference to this was made in Unnithan, 1961. Yamaguti, 1963 however, limits the family assemblage with the type genus and the defenition also is different from those used in the present rationale.

Protohaptor retained by adults only in *Carangiamata*. The microcotylid clamps are modified in at least three different ways, but the sucker-types are on the "opened box" plan, in which the rami of both jaws contribute to the frame. The secondary growth stimuli are expressed in the increasing modification of the clamps proximally, accompanied by an increase in their size, but these stimuli are imposed differentially on the two clamp-rows; the body/haptor axial tissue is not involved in the secondary growth, even when there is a metahaptor (the clamp-frills being usually adherent to the body proper, in contrast to Pyragraphorinae). Type genus *Heteromicrocotyla* Yamaguti, 1953.

Heteromicrocotyla Yamaguti, 1953 — Microcotylid clamps on unequal body-frills of entirely different units: the shorter row has the pyragraphorus-type of modification with 12-25 pedunculated clamps, and the longer sessile row 19-35 open suckerclamps which, though the rami of both jaws contribute to the frame, have opened more like a fan than a box, the ventral jaws (forming the 'lid' of the box) are more laterally spread and their shoulder pieces form two articulating arches anteriorly, while posteriorly their tips overlap the much smaller dorsal jaw-rami; the ventral arm of the median spring is greatly expanded distally forming two arched anterior supports for the sucker, the dorsal, now posterior end of the spring is more narrowly bifurcated, but the form of the spring varies in different species and may appear 'X'-shaped, rather than almost 'T'-shaped in the genotype (see Text-fig. 6D). There is a spiny eversible cirrus in a muscular sac and the atrium is armed with up to 3 groups of more slender spines. A large pre-ovarial vesicula seminalis is characteristic and is sub-lateral, probably always on the side of the long (sessile-) clamp-row, both of which may occur on right or left of the worm (Unnithan, 1961). The testes are numerous, usually more than 20 and up to 155. The single dorsal vagina may have an armed vulva, or gland-cells and radial muscles alone: the duct leads to the vitelline reservoir or to one of its lateral ducts. Genotype: *H. carangis* Yamaguti, 1953 from *Caranx* sp. from Macassar, Celebes. Two new spp. *H. vaginispina* and *H. polyorchis* on *Caranx malabaricus* (Bl. & Schn.) are described by Unnithan (1961) from Kerala, India.

Heterapta Unnithan, 1961 — Described fully elsewhere, is erected for what are probably two distinct species of Heteromicrocotylinae from Indian *Chorinemus* spp. The second species is *"Diplasiocotyle" chorinemi* Tripathi, 1956, which is certainly not congeneric with *D. johnstoni* Sandars, 1944 — an atypical microcotylid from an Australian mugilid fish. *Heterapta chorinemi* (Tripathi 1956) comb. nov. on *Chorinemus tala*, Cuv., from the Mahanadi Estuary, NW. Bay of Bengal (Tripathi '56: 235, fig. 2 *a-c*) and the genotype, both show a unique development of a metahaptor: a secondary growth stimulus has affected both clamp-replication axes equally, but has not involved the haptor/body axis: while the body itself is extremely elongated, the secondarily modified sucker-clamps of the metahaptor are in almost sessile rows along its ventro-lateral fields for half to nearly two-thirds its length. Doubtless the adhesion to the gill-surface of this long haptoral region, and the resulting traction, has been responsible for the shifting of the gonads into the relatively short field immediately in front of the proximal sucker-clamps. The euhaptor on the tapered tip of the body has not retained the protohaptor, and has its clamp-rows closely crowded together: 5 to 7 pairs of only slightly modified 'closed' microcotylid clamps, rather more stout and square than the typical. Clearly there has been some secondary replication here from the primary 4 pairs, but this has been interrupted and the formative zone has shifted forwards leaving (in the genotype) an isthmus devoid of traces of clamps. The meta-haptoral stimuli have resulted in producing an entirely different, open-sucker type of clamp, which has "opened like a box" with subequal quadrants bordered by the jaw-rami and supported along the hinge-line by the shoulder-pieces of the ventral jaw and the thickened anterior edge of the microcotylid clamp: the spring has become articulated and thickened as the meridional support for the sucker (see Text-fig. 6C). The most distal of these clamps may show a transitional form from the closed to the open type. The metahaptoral sucker-clamps increase in size gradually to the proximal third of their rows, then show a slight diminution, sub-equal in number 37-41 on either side, they may retain some power of reclosing their jaws, since they are well supplied with muscles (Tripathi, fig. *2c*). There is an eversible cirrus, when retracted its graded curved spines lie in 2 lateral ranks decreasing in size anteriorly, and deep in the sides of the cirrus-pouch are two very long rod-like spines (doubtless protrusible through the otherwise unarmed atrium as vaginal dilators). The vagina opens in a median dorsal pore, unarmed, about 5 times the length of the cirrus-pouch behind the bifurcation of the gut : at this level, the crural branches and vitellaria begin, and continue posteriorly to the last quarter of the metahaptoral region, whence the crura continue unbranched to their confluence at the end of this region (see Unnithan (1961) for genotype *Heterapta heterapta,* since Tripathi's figure lacks these details).

Dicotyle Tripathi, 1959 (Syn. *Bicotyle* Tripathi 1956—orthography emend 1959: 128) — Genotype *D. stromatea* (Tripathi, 1956) comb. nov. (Syn. *Bicotyle stromatea* Tripati, also as *B. stromatei* Tripathi, 1956 : 238) on *Stromates cinereus of Day* (=*Pampus argenteus* (Euphr.)) from Puri, Orissa, Bay of Bengal: a second species (*D. vellavoli*) is described from another Stromateidae *Chondroplites* (*stromateus*) *chinensis* (Euphr.), from Kerala, by Unnithan, 1961. The ovoid flattened body may have an elongated neck, constricted at the vaginal zone below the genital atrium, at the end of the oesophagus, which may be diverticulate. The asymmetrical clamp-rows are unequal body-frills in the posterior third: along the markedly convex side, the longer row of stout squarish microcotylid 'closed' clamps have cuticular ridges across their ventral walls (34-40, usually on the right side); the slightly shorter row- on the less convex side, consist of 10-17 larger and partly opened sucker-clamps : opening 'like a box', but not completely, the rami are thickened and simplified into 'C'-shaped arcs, and the spring is expanded at the ends and has perforations for the muscles. These clamps increase in size proximally, the first-formed (distal) clamp is very small and may be less than the microcotylid clamp opposite to it, the tip of the body is quite bare, the protohaptor, at least, being shed in earlier life. The outstanding feature of *Dicotyle* spp. is the reticulate intestine (though not mentioned for the genotype, its occurrence is inferred by Tripathi making *Microcotyle reticulata* Goto, a congener). The testicular field is partly embraced by the haptoral frills, causing a slight somatic asymmetry, due to torques set up by the pivoting in the feeding postures; testicular follicles in several rows, so that they have some freedom of relative movement during body-twisting — a distinct advantage of numerous small follicles over a few large follicles. There is a genital corona of strong spines (certainly not a cirrus) which may or may not be part of protrusible penis. The vagina is at the constriction of the fore-body, dorsal and cuticularized distally, either in irregular fimbrae and folds or with a circlet of teeth: it is single throughout and passes direct to the ootype.

Dictydenteron reticulatum (Goto 1894) comb. nov. (Syn. *Microcotyle reticulata* Goto, 1894; *Bicotyle reticulata* (Goto) Tripathi 1956), is the genotype of this newly erected genus. Its systematic position is problematic, since no difference was mentioned by Goto between the clamps of the unequal rows, other than those of the shorter row being about three times the size of the doubly numerous clamps in the longer row: on this evidence alone, it might be placed in Heteraxininae, on analogy with *Zeuxapta* and *Gonoplasius;* but in *Dictydenteron* the shorter side cannot be regarded as inhibited, since its clamps are larger. In view of its close similarity to *Dicotyle* particularly in the otherwise unique reticulate intestine, it must represent a transitional genus in Heteromicrocotylinae. An additional circumstantial reason is that it occurs on *Stromateus argenteus* Euphr. in Japanese seas. Apart from the clamp-type difference from *Dicotyle, Dictydenteron* has a cup-like genital atrium with a double corona of spines, probably the inner belonging to the penis; there is an unarmed vaginal pore leading to two ducts which enter the vitelline ducts rather than a single vaginal duct passing direct to the ootype: differences which are probably of more than specific rank.

Carangiamata gen. n. — erected for *Cemocotyle sagae* Manter & Prince, 1953 from *Caranx* sp. from Suva, Fiji: because both the structure of the clamps and the lack of a metahaptor exclude it from Cemocotylinae. It does, however, retain its protohaptor, with the usual 3 dissimilar pairs of larval hooks: but the euhaptor shows immediate differential growth-stimulation, both in intensity and in kind on each side: the haptor is an asymmetrical extension of the body-axis, but there is no lateral growth on one side comparable to the wing on the other which forms the postero-lateral end of the body, fringed with grapnel-like clamps (appearing like glochidia in profile view). On the straight side is a shorter row of 6 similar clamps of about twice the size of those in the opposite row: slightly different, however, since the ventral jaws are here much longer than the dorsal, and their rami swung apart as grapnel-hooks (M. & P.'s fig. 8), but both jaw-rami, dorsal and ventral are sharply pointed and can act as hooks as well as clamp-jaws. Neither of these clamp-types is quite like those of *Cemocotyle* nor the more asymmetrical clamps of *Xureliphilus elongata,* though the appendix on the dorsal arm of the median spring is a double in-curved filament rather like that in *Megamicrocotyle,* and there are also fine ridges on the capsule walls, at least in the larger clamps. The spherical oral pouches are very wide apart and a similar-sized pharynx is behind them. The penis is unique in being a thickened rigid tube (apparently without muscular bulbs as in *Kannaphallus* Unnithan, 1957) with conical apex protrusible through a round muscular genital atrium. The vagina was not seen. Monotypic genus with *Carangiamata sagae* (Manter & Prince 1953) comb. nov.

CEMOCOTYLINAE subfam. nov.—Heteromicrocotylidae with atypical microcotylid clamps usually only on the unilateral metahaptor: the larval haptor and euhaptor having apparently nearly normal unmodified microcotylid clamps. Except in *Megamicrocotyle,* the euhaptor is deflected laterally as a postural effect of the development of the more powerful clamps of the unilateral metahaptor. This is a common form of asymmetry in Axinidae also: the tendency of the body to be bent parallel to the longest line of attachment along the gill-lamella—as was so nicely demonstrated for various forms by Llewellyn (1956 *a*, pl. 2). Of the 4 genera, three occur on Carangidae and one on *Chirocentrus dorab* (Clupeiformes).

Cemocotyle Sproston, 1946 — The symmetrical euhaptor is a laterally deflected triangle, with rows of about 11 square microcotylid clamps, practically equal in size, immediately in front of the short protohaptor with 3 typical dissimilar pairs of larval anchors, and succeeded on one side only by the thick flange of the metahaptor. This is a perfectly straight shelf-like projection adherent to the side of the body proper to half way up the testicular zone, bearing in a close row some 26 larger clamps of the "muzzle", or rather "grapnel"-like, type. These diminish in size proximally: they are all twisted on their short pedicels to the profile view (as also in *Carangiamata* and the next two genera). Both jaws are slender and convex, the one considerably overlapping the other, both with sharply pointed rami acting like slender claws — these are much longer and more prong-like than those of *C. sagae* Manter & Prince. They have reported on their re-examination of the type and paratype of *Cemocotyle carangis* (MacCallum, 1913) Sproston 1946, from *Caranx crysos* (Mitchill) from the American North Atlantic, and largely confirm the original description, but adding a third small pair of protohaptor hooks; they contend that the spiny sucker surrounding the vagina is ventral (?). MacCallum stated that this ring-sucker was ventral, but that the (figured) vagina has a dorsal unarmed pore slightly behind this. The round oral suckers occupy the corners of the wide flat forehead, and there is a triangular cuticularized genital atrium with lateral and median spine-groups, though the penis is unarmed. Hargis (1956 (xi) : 154, 159) would include this species in Heteraxininae, but this is inadmissible since the clamps are not uniformly microcotylid, and a metahaptor is never present in Axinidae. He found it on the type host in Alligator Harbour, Florida.

In my opinion, the evidence fully establishes the genus, which remains monotypic with *Cemocotyle carangis* (MacCallum, 1913) Sproston, 1946.

Xureliphilus gen. nov., erected for *Axine elongata* Meserve (1938, 61, figs. 53-58) found off Secas Island, Panama, E. Pacific, on *Xurel melampygus* Cuv. This is removed from Heteraxine for the same reason as is the next species: the possession of a unilateral metahaptoral flange with abruptly modified clamps.

In *Xureliphilus elongatus* (Meserve) comb. nov., though the protohaptor is lost, probably the 3 pairs of small distal microcotylid clamps are the primary clamps of the larval haptor, and the euhaptor is represented by the succeeding 3 pairs of larger microcotylid clamps on either side. Then on one side there is an abruptly projecting wide flange, the metahaptor, adherent to the body except at its extreme anterior end, and bearing a close row of (18) *Cemocotyle*-type clamps, again twisted into profile position in ventral view. These metahaptor clamps have a double internal asymmetry ; the ventral jaws are longer than the dorsal, and the rami of both are much longer on one side than on the other (the shorter being more convex, so that their side of the clamp is the wider). In *Cemocotyle* the prong-like ventral jaws are sigmoidally arched and sharply clawed, but in *Xureliphilus* the inwardly bent ends of the ventral jaw are expanded as notched knobs. The vast development of the uterus (at least half of the body-length and width), packed with bi-filamented eggs, perhaps obscured the male terminalia, since only a muscular oval was seen (referred to as the genital atrium, but without mention of its contents), which may have been the uterine pore. A vagina was not seen. The aseptate oral suckers are extremely far apart, and the wide forehead has a median conical papilla.

There is a wide calibre loop internally to the euhaptor, with a branch along the base of the metahaptor (and here a transverse commissure between the two lateral trunks) giving off thinner radial branches to each clamp-base. This is referred to as part of the nervous system, but it is strongly reminiscent of the "semi-circulus haptoris", so conspicuous also in some *Opisthogyninae* (see Unnithan, 1962), and in Axinidae Unnithan (1957), which is suspected of being a water-vascular system ancillary to the clamp mechanism (see also remarks under *Pricea* infra).

Tripathiana gen. nov., erected for *Heteraxine minuta* Tripathi, 1959, found on *Megalaspis cordyla*, from Puri and Chilka Lake, Orissa, Bay of Bengal. *Tripathiana minuta* is characterized by the development of a powerful unilateral metahaptor, which is practically all free from the body and bears atypical clamps. The obliquely truncated posterior end lacks the protohaptor, and it is deflected laterally from the body-axis as in *Cemocotyle* and *Xureliphilus*. The euhaptor is asymmetrical though the sides bear a similar number of clamps (10/13), which are squareish, typically microcotylid ; but on the shorter side they increase in size slightly, while on the long side the 2nd. to 5th. are larger than the others but smaller than those opposite to them on the short side.

The metahaptor has a wide fleshy margin bearing closely set modified longer clamps at right angles to the others (profile view only, in face-view of haptor). These clamps are twice as long as the euhaptor clamps but only about as wide ; and their jaws, though hooked, are sub-equal. Of these eleven clamps, the anterior 4 or 5 are uniformly smaller than the others. The blunt rounded head is about the same width as the rest of the cylindroid body. The unarmed dorsal vagina was obscured by dense vitellaria ; the genital atrium is unarmed, but the penis has a corona of 6 hooks with broad tapering handles. It was found on 3 occasions when an average of nearly 70% of the hosts were infected.

Megamicrocotyle Tripathi, 1956 — Originally monotypic, with *M. chirocentrus* Tripathi (1956, 236, fig. 1 *g-k*) on *Chirocentrus dorab* (Forsk.), from Puri, Orissa, Bay of Bengal: a closely allied species discovered on the same host in 1955 and described by Unnithan (1961), in Kerala (Arabian Sea), and *Lintaxine microcotyla* Manter & Prince from 'a ribbon-fish' in Fiji, now form a highly compact genus; it is even probable that re-examination of the types may suggest the Indian examples being subspecies. Outstanding is the extreme difference in the clamps in the two rows, both in size and in modification of the microcotylid type; also, there is no difference in the clamp shape as the euhaptoral row passes into the unilateral metahaptoral wing, such as is seen in *Tripathiana.* The haptor is an extension of the body-axis though set off from it by a tapered rather short pedicel which contains no crural branches nor vitellaria, but the unbranched intestinal crura extend for at least two thirds the length of the haptor to slightly different levels. The larger stalked clamps have a unique modification of the ventral jaw-rami: distally each has an ankylosed horizontal bar on its tip, recalling an anther of a flower stamen. I feel that the temptation must be resisted to homologize these bars or reflexed flanges with the braces of the gastrocotylid clamp and for three reasons; (1) they are not connected in any way with the dorsal jaw-rami, nor with the appendages of the median spring — relationships invariably found in the true gastrocotylid structure; (2) they are not represented by any vestige in the sessile clamps; (3) the sessile clamps, while sometimes being completely opened sucker-clamps, are not of the gastrocotylid sucker-type, for example in *Lintaxine,* but are perfectly conformable to the opened-box type found in *Heterapta* (compare Text-figs. 6B & F). In the former the gastrocotylid sucker-clamps are seen to open always like a book, and the dorsal jaw-rami take no part in the sucker-frame. The development of the appendages on the dorsal arm of the spring is microcotyloid rather than gastrocotyloid—there are no dorsal lamellae developed, but only a narrow bifurcation, the arms of which come together in a pointed loop far anterior to the tips of the dorsal jaw-rami, which are long and gaping like grapnel-hooks. The ventral wall of the capsule is finely striated, but there are no true ribs as in gastrocotylids or some Pyrographorinae (*cf.* Text-figs. 4, 5C & 7F). In Tripathi's figure (1956, *lh*) the bars from the ventral jaw-rami are shown fused together as a single bar, but in the other species they are quite separate and unconnected with the end of the spring—a re-examination of the Bay of Bengal material is indicated. The sessile clamps are usually only 8-9 μ in diameter (Tripathi states 15-19 μ), whereas the larger are 40-60 μ, and in the proximal four-fifths of their row they are placed well within the margin of the ventral side of the euhaptor. Their structure is simplified microcotylid with strong 'C'-shaped jaw-rami, partly opened as in *Dicotyle,* or with the ventral jaw opened back like the lid of a box as in *Heterapta,* the spring having wide-splayed ends and the hinge-line cuticularized which together form the cross-wise supports in the base of the sucker-clamp: they are well supplied with muscles into the body of the haptor, which are seen as ranks of striae in the ventro-lateral field of this nearly straight row. The distal clamps are subsessile on both sides, at the tip there is a minute lobe perhaps representing the vestige of the protohaptor, but the four pairs of primary (larval) clamps are no longer distinguishable from their successors (nor were they in *Heterapta* or *Cemocotyle*) but the distal 10 or 14 small and the distal 5 large clamps are, respectively, slightly larger and smaller than the others, and on short stalks (the smaller being nearly closed). After these distal subsessile small clamps Megamicrocotyle Tripathi shows a relatively long bare gap in the row, which continues with the submarginal row : in both the other species, also, there is a change in disposition of the small clamps at this level : the distal dozen or so are strictly marginal like the larger clamps. The latter then have longer stalks, with a marked increase in stalk length and size of clamp when the row departs as the metahaptoral free wing, bearing about 14-18 (or about a third of the total number of) large clamps.

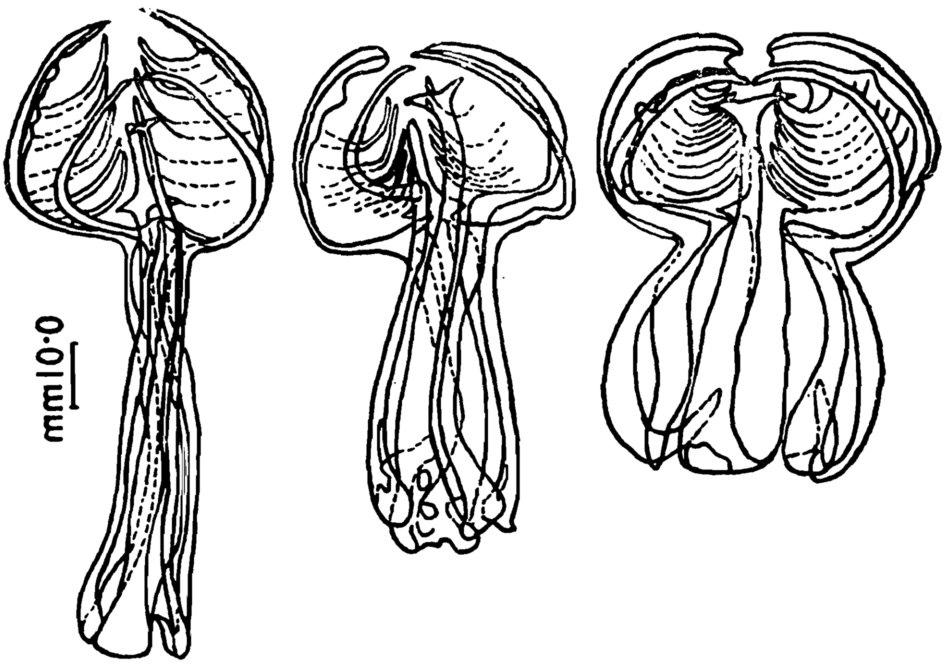
The anterior end is slightly expanded and the oral pouches almost transverse in its angles, the pharynx is about half their size and the mouth appears to be protrusible, much as in *Cemocotyle* and *Xureliphilus,* without very conspicuous gland-organs. The male terminalia are unique: in the Indian species there are two more or less elongated triangular plates on either side of a highly cuticularized flask-shaped penis (the 'hooks' figured by Tripathi appear to be equivalent in position to the thickened walls of the penis seen in profile in the new species); proximally there is a strong muscular bulb thought to act as a compressor in ejaculation. In the Fijian *Megamicrocotyle microcotyla* (Manter & Prince, 1953) comb. n., the male apparatus seems to show clear specific differences: there are the lateral (spinose) plates and a forward-pointing transverse plate bearing a row of small sharp spines (atrial structures), the muscular bulbous penis has laterally graded thorns on its head. The vagina is similar in all, and unusual in being in the ovarian zone and short, leading directly to the receptaculum seminis: the vulva is provided with a hood and cuirass-like transverse plates, their diameter, of course, being the same as the flattened anterior ridge of the atrium masculinum, which would be anchored by the vaginal plates, but the vaginal pore is minute at the posterior end of the 'vulval ovoid' (see Unnithan, 1961); in *M. microcotyla,* the pore is larger and the hood more extensive.

In spite of the extreme smallness of the one row of clamps this cannot be interpreted as due to inhibitory influences, but rather to extreme stimulation in replication (56 to 90 of them), and the stimuli are manifest on the other side by the increase in size, stalk-length and finally the metahaptoral wing. The host of the Fijian material was not named, but it is perhaps unlikely that the Dorab would be described as a 'ribbon-fish' in spite of its elongated body, it is altogether stouter than the Trichiurids, for instance. The original placing in *Lintaxine* is not understandable, particularly on the host basis, since *L. cokeri* is from a freshwater sciaenid, and no sciaenid fishes are known to occur in Fiji Islands.

PYRAGRAPHORINAE subfam. nov. Heteromicrocotylidae which have morphologically bilateral symmetry, but the bilateral metahaptor being entirely free from the body proximally (ventrally) is, as a postural effect, twisted through a right-angle, and still in line with the distal euhaptor, forms a "T"-shaped tail. Such a "fish-tail" effect is also common in several Microcotylidae (other than Microcotylinae) also in *Pricea,* and to some extent in *Thoracocotyle crocea* (Gastrocotylidae). But unlike these genera the clamps of Pyragraphorinae are specially modified, in some ways similar in all three known species. Other characters in common are the biloculate spiny oral suckers (round and simple in the other subfamilies), and the dorsal vagina, which like the penis or cirrus may be cuticularized or not. Parasites of Carangidae.

Hargis (1956 (x): 448-452) reports on a re-examination of the type material of the two older species and describes a new species, all of which he considers congeneric. In view of some differences of generic rank, I prefer to consider *Pyragraphorus* monotypic, and to unite the second and third species in a new genus dedicated to our prolific colleague: *Hargisiella* gen. nov.

Pyragraphorus Sproston, 1946 — Pyragraphorinae in which there is a more or less abrupt change in clamp-type from the euhaptor to the metahaptor: the clamps on the latter are of the pyragraphorus (fire-tongs) type, having the anterior parts of the rami of both jaws drawn out into a handle: this modification *in transit* is clearly figured by Bychowsky & Nagibina (1959 fig. 21) (Text-fig. 4 herein) and they also show for the first time, the development of rib-like thickenings from the capsule wall becoming free medially as inward-pointing curved claws. The clamp figured on the right shows a deep ridge-like lip of the ventral jaw-rami: this is significant, since it helps to explain an anomaly in both 'Macallums and Hargis' figures of the distal (=Euhaptor) clamps. These less modified clamps have the jaw-sclerite lip bent



TEXT-FIG. 4. *Pyragraphorus* sp. progressive modification of clamps (from Bychowsky & Nagibina, 1959).

at a right angle posteriorly, and evidently in optical section it appeared as a double sclerite. At first glance the American figures recall a gastrocotylid clamp with the two extra posterior sclerites, but whereas the oblique "braces" of the gastrocotylid clamp occur internally and articulating with the dorsal jaws, these figured for *Pyragraphorus* are posterior and external to the rami of both jaws. I conclude, therefore, that the two extra sclerites in the American figures are optical illusions resulting from the deep bent jaw-lip, and the clamps are all essentially microcotylid, albeit highly modified.

Hargis claims that there are two kinds of modified clamp in the euhaptor (his "dorsal lobe" — an inconvenient term since it has only postural and not strictly morphological import): in the more distal clamps (Hargis 1956: fig. 23) there is a strong internal asymmetry, the abaxial jaw-rami are grossly thickened and more convex, and in others in the euhaptor (more proximal clamps ?) he claims to have found developments like those in *Hargisiella* spp. particularly in respect of the hole through the elongated dorsal end of the median spring — to admit the tendon of the adductor muscles. This hole has shifted to the middle of the spring in the more proximal of the pyragraphorus clamps as in Bychowsky & Nagibina's figure (Fig. 11): compare Fig. 1 in Sproston (1946) for various types, and Llewellyn (1956 *b*, fig. 1) for *Plectancotyle*.

In *Pyragraphorus*, besides the dissimilarity between the clamps of the euhaptor and metahaptor, there are three generic characters which are absent in *Hargisiella:* lateral diverticula in the oesophagus, and a spiny eversible cirrus in a long muscular sac along with an internal vesicula seminalis (see Hargis 1956, fig. 22); furthermore, the receptaculum seminis immediately behind the cuticularized vagina opens into the right lateral vitelline duct. This genus remains monotypic with *Pyragraphorus pyragraphorus* (MacCallum & MacCallum 1913) Sproston 1946: on *Trachinotus carolinus* (Linn.), probably from the North American Atlantic.

Hargisiella gen. n., erected for *Pyragraphorus hippos* Hargis, 1956 (designated genotype, since it is the better described and figured) Text-fig. 5F, and *Pyragraphorus* (*Microcotyle*) *incomparabilis* (MacCallum 1917) Hargis 1956: the former on *Caranx hippos* (L.) from Florida and Texas, and the latter on *Caranx ruber* (Bloch) from Florida. The symmetrical euhaptor is again the continuation of the body-axis, but growth potentials in the long-axis of the haptor are evidently much higher than in the hind-body, for subsequent growth continues independently, nevertheless receiving branches from the intestinal crura as the new lobe leaves the body. The crural branches join in a median, secondarily branched, crus in the metahaptor (proximal and ventral lobe of the haptor), just as they do in the euhaptor: neither testes nor vitellaria enter either euhaptor or metahaptor. Growth potentials are so strong, at least in the genotype, that the metahaptor can be double the length of the euhaptor — in *Pyragraphorus* the two parts are practically equal. *Hargisiella* however, does not show a change in clamp-type between euhaptor and haptor — the pedunculated elongated clamps are all alike, and they are comparably modified in both species. In *H. hippos* there is a marked internal asymmetry (according to Hargis, 1956, fig. 20) the more elongated dorsal jaw-rami do not meet in the middle line, one side is more bent and lipped than the other distally but proximally the other side is the more bent before the articulation under the shoulder of the ventral jaw. The dorsal arm of the median spring is elongated to the jaw-lip where it expands and has a transversly oval hole (Text-fig. 5E).

In *H. incomparabilis* the whole clamp is much stouter and longer in proportion to its width (Text-fig. 5D), and the dorsal jaws are a little longer than the ventral again having asymmetrical rami. The outstanding feature of this clamp is the pocket-like expansions of the dorsal arms of the ventral jaw-rami which form the shoulder articulation, and one side is larger than the other here. The dorsal arm of the median spring is elongated and evenly wide, having a round hole at its end.

The abaxial-adaxial asymmetry of the clamps of *Hargisiella,* and to a less extent those of the euhaptor of *Pyragraphorus,* suggest an advanced level of adaptive evolution comparable to that in Opisthogyninae and Gotocotylinae (Gastrocotyloidea), but in the latter internal asymmetry of the clamp has reached its zenith.

In *Hargisiella* there is an eversible cirrus but no internal vesicula seminalis, and there is no armature whatever near the male terminalia. The mid-dorsal vagina has a cuticular folded lining in *H. incomparabilis,* but it is not cuticularized in *H. hippos,* where the short duct leads direct to an anterior bridge between the lateral vitelline ducts at the anterior fourth of the body, and they do not form their short median duct until the mid-ovarian zone at the middle of the body. Some vitellaria enter the euhaptor only in *H. incomparabilis.*

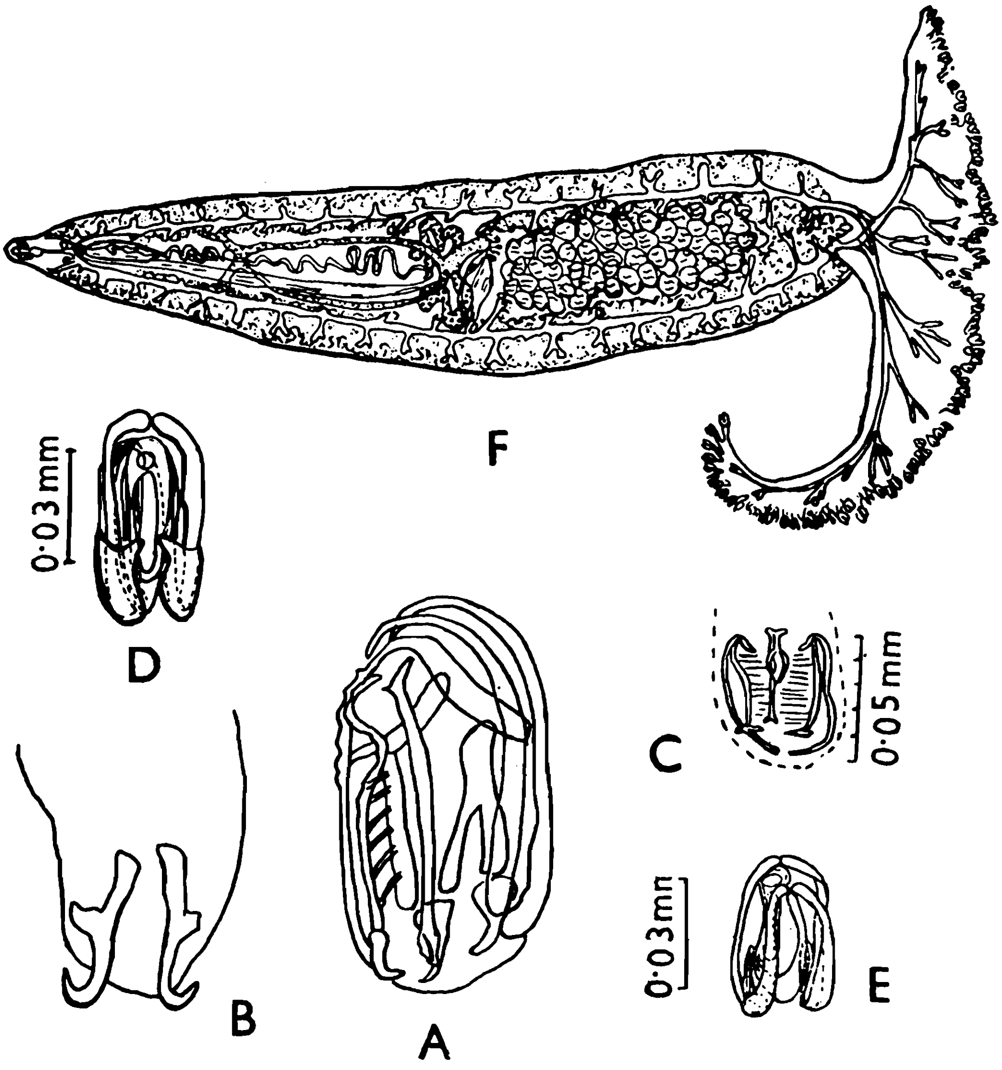
GASTROCOTYLOIDEA Price 1959

(Syn. Gastrocotylidae Price 1943 + Discoctylidae *s. lat. partim*)

This superfamily was originally erected in the first draft of this paper, to consolidate some of the variety of new forms which have been discovered during the past few years. Price (1959) has published this name for a similar assemblage, but which he subdivides more according to the older views than I do. In common, they all have microcotylid (discocotylid) type of clamps with the addition of a pair of oblique frontal braces.

These, seem to have been derived from the appendages on the end of the ventral arm of the median spring, often present as a bifid appendix but of no structural importance in various species of Microcotyloidea (Text-figs. 1B, 3A). In Anthocotylidae Bychowsky, 1957, they are being transitionally incorporated as definitive sclerities in the clamp mechanism. In some subfamilies of Gastrocotyloidea further additional sclerites are incorporated, apparently derived (*a*) from the anterior end of the dorsal arm of the median spring (in Priceinae and Gotocotylinae *s. str. nov.*), and (*b*) from the rib-like thickenings in the (mainly ventral) wall of the capsule, which occur rather spasmodically in many species of the Order Mazocraeidea Bychowsky, 1957, but in some subfamilies of Gastrocotyloidea they are more highly developed and contribute in various ways to the essential clamp-mechanism (Thoracocotylinae & Gotocotylinae).

Gastrocotyloidea echo, in several keys, the main evolutionary calls of all the rest of the Suborder Discocotylinea Bychowsky 1957 ; so that to satisfy logical consistency, a parallel suborder would be necessary for them. I hesitate to take this step, however, until it can be supported by more evidence from ontogenies. Llewellyn (1967 *a*) described briefly the larvae of *Gastrocotyle* and *Pseudaxine,* and found the shape of the terminal anchors to be quite different from other Discocotylinea, including *Microcotyle* spp. ; he concluded, with every justification, that Sproston (1946) was in error (*inter alia*!) in uniting Gastrocotylinae with Microcotylinae in Microcotylidae.



TEXT-FIG. 5. A. *Gotocotyla sawara* Ishii, 1936, a single clamp, and B. protohaptor with one pair of anchors (both from Ishii, 1936); C. *Megamicrocotyle* (Manter & Prince, 1953) 'comb'. nov., ventral view of a large clamp (from Manter & Prince, 1953); D. *Hargisiella incomparabilis* (MacCallum, 1917) gen. nov., dorsal view of clamp; E. *Hargisiella hippos* (Hargis, 1956) gen. n., clamp ventral view, and F. the whole worm, ventral view (figs. B-F from Hargis, 1956).

In attempting to classify the Gastrocotyloidea group, I have used the same principles as before in this paper, at least in separating the higher taxa: but at present each higher category here is one rank lower than in the rest of Discocotylinea. The family Gastrocotylidae *s. str. nov.* corresponds to the superfamily Microcotyloidea (Unnithan, 1957) *s. str. emend.,* in that it represents subfamilies in which the growth of the haptor is potentially unlimited. Among the subfamilies, difficulties arise in the maintenance of a strictly logical parallelism: there are 4 distinct clamp-types within the "gastrocotylid-type" variants, but none of them corresponds with the grossly remodelled clamps in Heteromicrocotylidae. The clamp variants are morphologically more fundamental, but not so striking in appearance. The haptor which bears them shows sometimes inhibitory influences as in Axinidae Unnithan, 1957, (*Gastrocotyle* and *Pseudaxine* are both "Monaxinid" genera), and sometimes secondary growth-stimulation, resulting in a unilateral or bilateral metahaptor, which tends to grow anteriorly (and ventrally if bilaterally symmetrical as in *Pyragraphorus, Pricea and Thoracocotyle*). Since these growth inhibitions and secondary stimulations occur with 4 different types of clamps, they have been subordinated as taxonomic criteria, to those of clamp-type notwithstanding their striking effects, and probably deep-seated origin (differential inhibitions in growth of haptor are family criteria in Microcotyloidea — Unnithan 1957).

It is interesting to note, without going into a detailed analysis at this stage, that among these more highly evolved Discocotylinea, the Heteromicrocotylidae and Gastrocotylidae, there is a parallelism in their parasitizing the more highly evolved group of fishes: the former predominantly on Carangidae, and the latter on Scomberomoridae (=Cybiidae *auct.*)

GASTROCOTYLIDAE Price 1943 *emend.*

(Syn. *Gastrocotylinae* Sproston, 1946)

Gastrocotylidae shares with other Gastrocotyloidea the character of the extra pair of the sclerites (oblique braces) in the distal (posterior) region of the clamp capsule, and is distinguished by the potentially unlimited growth of the haptor.

The five subfamilies, distinguished by structural modifications and/ or the presence of accessory sclerites in the clamp structure are: Gastrocotylinae Sprostom (1946), *partim, emend.;* Thoracocotylinae subfam. nov.; Priceinae Chauhan (1953) *partim, emend.;* Gotocotylinae subfam. nov. and Engraulicolinae subfam. nov.

GASTROCOTYLINAE Sproston 1946, *partim, emend.*

Gastrocotylidae in which the basic gastrocotylid clamp structure is unmodified. Other characteristics, except for the ovary with its distal limb descending, are all highly variable. 5 genera:—*Gastrocotyle* v. Ben. & Hesse, 1863 ; *Chauhanea* Ramalingam, 1953 ; *Yamaguticotyla* Price, 1959 ; *Churavera* Unnithan, 1968 and *Eyelavera* Unnithan, 1968.

Gastrocotyle v. Ben. & Hesse 1863: Gastrocotylinae in which the haptor has sustained a complete unilateral inhibition (as in Monaxininae, Axinidae), an inhibition which has affected the haptor-body axis immediately after the protohaptor. The result is a single euhaptoral flange adherent to the body, on one side only: the body axis has not lengthened infront of the protohaptor, which is retained as a short lappet with, typically, 3 dissimilar pairs of larval anchors (see Llewellyn 1957: figs. 12, 22). The clamps are internally symmetrical, but the ends of the median spring are atypical in *G. trachuri* v. B. & Hesse, the end of the ventral arm may be bifurcate and articulate with the dorsal jaw-rami (*vide* Sproston 1946, fig. 108 *d, e*). In *G. indica* Subhapradha (1951) however, there is shown what is called an "extra sclerite" on the dorsal end of the spring, like two convergent horns arising from a fine cross-bar: but comparing this with my own observations and those of Yamagüti (1938, fig. 37), both for *G. trachuri*, Subhapradha's 'horns' would appear to be the slightly thickened edges of the hole in the dorsal wall of the capsule which admits the adductor tendon and lateral muscles on the spring; and the cross-bar, in her fig. 8 *a*, might be a transverse fold in the wall, since it has no counterpart in Priceinae, in which veritable sclerities do arise as paired lamellae on either side of the tendon-hole. Until this question is re-examined in all three species, I tentatively assume that no extra dorsal sclerities are actually formed in the essentially simple clamp of *Gastrocotyle*.

The male terminalia consist of a simple muscular bulb with a crown of erect stout spines abruptly diamond-shaped or bifurcate at their bases, exactly as in *Psuedaxine ;* the nearby dorsal vaginal pore is unarmed. Genotype: *G. trachuri* v. Ben. & Hesse 1863, on *Trachurus trachurus* L. from English Channel. Noth Sea, and from Tarumi and Majsaka in Japan; other spp:— *G. japonica* Ishii & Sawada, 1938 on *Pneumatophorus* (*Scomber*) *japanicus* (Houttuyn), from Japan; *G. indica* Subhapradha, 1951 on *Caranx kalla* Cuv., from Madras, Bay of Bengal; *G. kalla* Unnithan, 1968, on *Caranx kalla* Cuv., and *G. kurra* Unnithan, 1968 on *Caranx kurra* Cuv. from Trivandrum, Arabian Sea.

Chauhanea Ramalingam 1953: monotypic with *C. madrasensis* Ramalingam, 1953 on *Sphyraena acutipinnis* Day, from Madras (Bay of Bengal), and by Euzet & Razarihelisoa (1959), on *S. commersonii* Cuv. from Madagascar: the symmetrical haptor is an extension of the body-axis, with a few more clamps on one side than the other (30-49/36-55); they are slightly longer than wide but the jaw-rami on one side are slightly thicker and more convex than on the other, an incipient internal asymmetry found also in Opisthogyninae. Growth stimuli in the long-axis of the haptor have been in excess of those of the haptor-hindbody but apparently confined to the clamp frill, and not producing anterior extensions (metahaptor). Here is the first example of a highly localized growth-stimulus: a double row of clamps on either side, beginning soon after the protohaptor — the hooks of which are lost in the adults of *Chauhanea.* Oral suckers aseptate; cirrus unarmed, opening immediately under the median vagina which has a finely dentate pore. *Chauhanea* is exceptional in the entire family in having testes parovarial, and an almost equal number post- and pre-ovarial.

Yamaguticotyla truncata (Goto 1894 — as *Microcotyle*) has been considered by Price (1959) to be a gastrocotylid, and type of his new genus. Originally found on *Pristipoma japonicum* and later by Ishii & Sawada (1938) on *Parapristipoma trilineatum* on both occasions from Japan (hosts considered by some to be identical), has only 10 or 11 clamps on each side of the short frill-like haptor ; genital atrium (? penis) said to be armed with 20 or more slender spines of variable length ; vagina unarmed, and polar filaments of egg long.

Churavera Unnithan, 1968: monotypic with *C. macrova* Unnithan, 1968, on the gills of *Euthynnus affinis* (Cantor) from Trivandrum (Arabian Sea): the haptor and clamps almost gastrocotylid with only the oblique sclerites and no accessory sclerites nor an appendix for the median spring. Riblike thickenings also absent in the clamp capsule. Haptor includes only the posterior half of the testes zone. Male terminalia is armed with a corona of hooks and a large ejaculatory bulb is present. Ovary is inverted 'U' shaped and testes numerous. Egg is large and vagina is absent. Parasitic on the gills of marine fishes.

Eyelavera Unnithan, 1968 : Another monotypic genus recorded by Unnithan (1968) on the gills of the Indian mackeral *Rastrelliger kanagurta* (Cuv.) at Trivandrum (Arabian Sea). The haptor forms a unilateral oblique frill of gastrocotylid clamps at the posterior third of the body, overlapping a part of the testicular zone. Clamps are heavily cuticularised with fleshy lips but no extra sclerites except the short oblique ones ; median spring has a broad ventral and vestigial dorsal arm. There are two well defined lateral vaginal pores. Ovary inverted 'U' shaped, testes though mainly postovarian there are few par-ovarian ones also. Male terminalia armed with hooks. The intestinal crura has long ramifying outer branches. Parasitic on the gills of marine fishes. Type species : *Eyelavera typica* Unnithan, 1968.

THORACOCOTYLINAE Sub-fam. nov.

(Syn. Priceinae Chauhan (1953) *partim*). Erected for *Thoracocotyle* MacCallum, 1913 (which was previously grouped with *Pricea* Chauhan and *Lithidiocotyle* Sproston, solely on account of the rib-like thickenings of the capsule-wall — a character common to numerous genera in other subfamilies), and for three newly recruited genera having essentially the same type of "open-sucker" clamp modification: *Dawesia* Unnithan, *Lintaxine* Sproston, and *Amphipolycotyle* Hargis.

The *gastrocotylid "open-sucker" clamp* is quite differently formed from that in Heteromicrocotylidae (Heteromicrocotylinae), which was a simple posterior-anterior opening, like the hinged lid of a box (discussed under *Megamicrocotyle*), where all four quadrants of the jaw-rami contributed equally to the effective frame of the sucker. In Thoracocotylinae only the rami of the ventral jaws contribute to the effective frame of the sucker. Incidentally, in Diclidophoridae (Choricotylinae it is only the abaxial ramus of the ventral jaw and the ventral arm of the median spring which frame the sucker. This clearly contrasting enlistment of sclerites for the sucker frame may be a highly significant systematic pointer (Text-figs. 6 D-G).

The gastrocotylid "open-sucker" clamp characterizing Thoracocotylinae is like an opened book : a lateral opening-out, in which the right and left moieties have been flung back, more or less flat against the supporting tissues. In the process, the median spring, freed from the restraint of the jaw-adductors, has opened out nearly straight and slid outwards and dorsally under the now shallow bowl-like clamp capsule, for which it provides the meridional brace. At the same time the pair of oblique braces of the original gastrocotylid clamp have also been thrust outwards and lie near the end of the spring on the posterior rim of the capsule. The dorsal jaws are also jettisoned from the sucker-frame, at first remaining at the sides of the frame (*Lintaxine*), and perhaps in a later phase of evolution, pulled medially to lie parallel with the oblique braces outside the dorsal anterior edge of the frame (*Amphipolycotyle, Thoracocotyle*). In the last, there is slight asymmetry and the concavity is strengthened by thickened ribs from the capsule wall. In all of these, the ventral jaw rami have their shoulder-piece bent back and towards the centre of the former hinge so that they form the two "C"-shaped halves of the frame.

Again, in this subfamily, there are very different displays of growth-potentials in the haptor: specialised stimulation in *Amphipolycotyle* (unilateral metahaptor with atypical clamps), unspecialized in *Thoracocotyle* (bilateral metahaptor, all clamps similar, but suppression of haptor-body axis), and a unique suppression of only the lateral axes of the haptor in *Lintaxine* (quantitative differential stimulation in the growth of the longitudinal axes of the haptor — clamp rows). In *T ovalis* Tripathi, the unusually wide body and posterior shift of the pivoting point combine to produce a somatic asymmetry reminiscent of that in *Vallisiopsis*. The protohaptor is apparently lost in the adults of *Lintaxine*.

Thoracocotyle MacCallum, 1913 is characterized by open ribbed sucker-clamps which usually show an incipient internal asymmetry (see Meserve's fig. 43): the 'C'-shaped rami of the ventral jaws forming the right and left halves of the frame joined by the widely forked ends of the opened median spring, while the vestigeal rami of the dorsal jaw, along with the oblique braces have been thrust out of the frame to lie against the anterior rim. The protohaptor is retained on the posterior end of the body: a stout lobe bearing the two posterior pairs of larval anchors, separated from the primary clamps by a short interval.

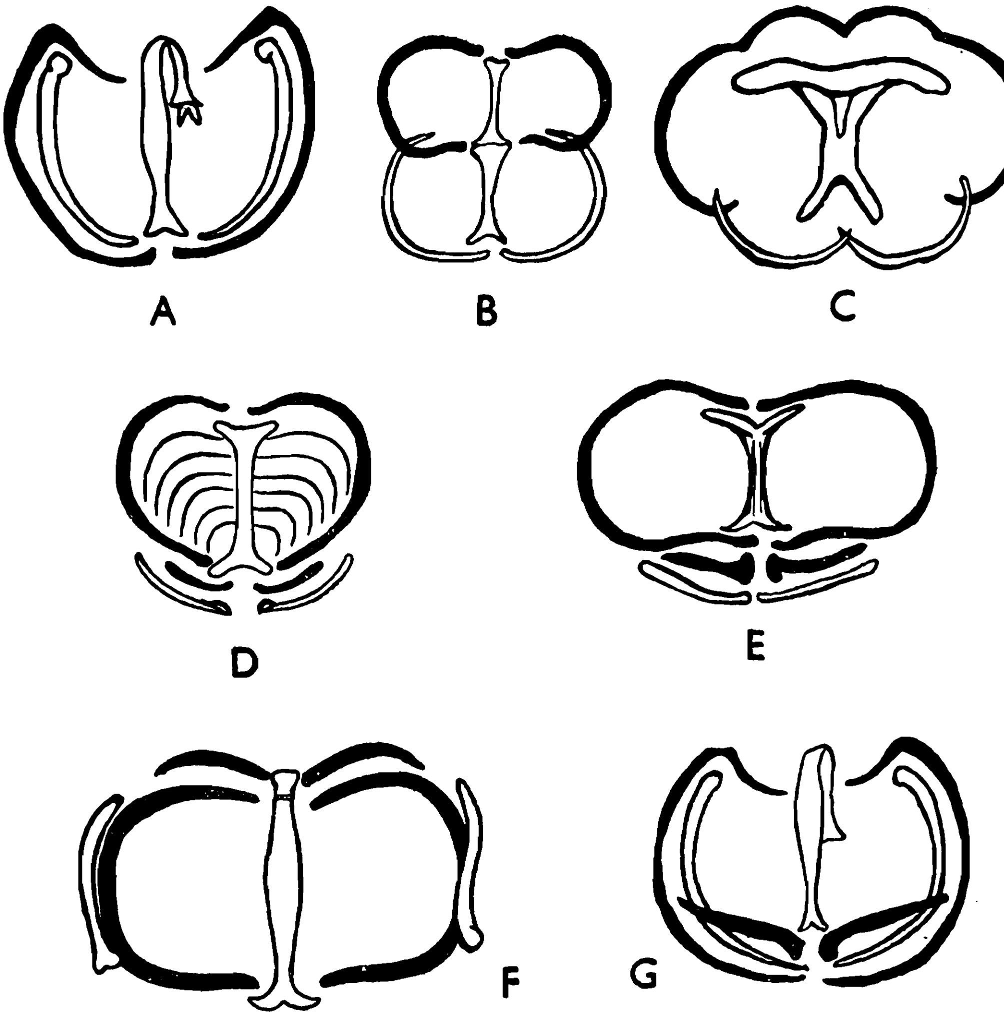
The testes are relatively large, 7-9 in single file in *T crocea,* but in *T ovalis,* there are hundreds of small spheroidal follicles packed in the intercrural field in the posterior half of the body proper. The penis and atrium are unarmed, the vaginal pore is just anterior to the ovarian zone, and (at least in MacCallum's material of the genotype, it opens ventrally) surrounded by muscles. It leads to a sac-like receptaculum seminis, which is large, pyriform in *T ovalis,* and has a reflexed duct from the apex back to the ootype, in both cases apparently independent of the vitelline ducts. Genotype: *Thoracocotyle crocea* MacCallum, 1913 from New York Aquarium on *Scomberomorus maculatus* (Mitchill), and from Florida by Hargis (1956: xii): (Syn. *T paradoxica* Meserve, 1938 on the same host in Mexican Pacific, at Tangola-Tangola); second species *T ovalis* Tripathi, 1959 (Syn. *T ovale* Tripathi, 1956) on *Scomberomorus guttatus* (Bloch & Schneider), from Puri, northern sector of Bay of Bengal, India.

Dawesia Unnithan, 1964: monotypic with *D. indica* Unnithan, 1964 on *Scomberomorus guttatus* (Bl. & Schn.) at Trivandrum, Arabian Sea. The genotype described and discussed in detail elsewhere (cf. Unnithan 1964) resembles *Thoracocotyle crocea* MacCallum, 1913 very closely especially in the nature of the haptor and clamp pattern. *Dawesia* however, has an elaborately developed armed penis, two lateral vaginae and its body organs do not extend into the haptoral zone.

Lintaxine Sproston 1946 : monotypic, with *L. cokeri* (Linton, 1940 as *Heteraxine* sensu Linton, non *Heteraxine* Yamaguti, 1938), on the freshwater Sciaenid *Aplodinotus grunniens*, Raf., from Fairport, Iowa, USA. Thanks to the re-examination of the type material by Manter & Prince (1953: 110, 112, figs. 18, 19), doubts about this genus, shared by Tripathi (1959: 129), are now dispelled. The unique feature of *Lintaxine* is the complete inhibition of lateral growth in the haptor (euhaptor), resulting in a morphologically posterior-anterior thick ridge directed obliquely laterally in with respect to the body-axis, or rather *vice versa* in the normal attitude of these Monogenea on the gill-filaments. This tapered fleshy end of the body bears two close sessile rows of "open-sucker" type of clamps. The growth on the right and left sides is controlled by quantitatively different impulses: while the rows are equally long, on the one side large wide sucker-clamps (10 of them, increasing gradually in size anteriorly, and on the other there are three times as many but only one-third the size and sub-equal, yet apparently of the same type.

The lintaxinid clamp-type (Text-fig. 6F) may represent an earlier stage in the evolution of the thoracocotylid clamp-type than even *Amphipolycotyle* (Text-fig. 6E), for though it is a stouter version, the jettisoned dorsal jaw rami remain on the edges of the sides of the frame formed entirely by the ventral jaw rami, while the oblique braces lie outside the frame on the posterior edge, though still attached to the ventral end of the median spring (which, as in related genera, forms the sole meridional support of the sucker). There are no rib-like thickenings braceing the cavity of the sucker in *Lintaxine* or *Amphipolycotyle*, yet these adhesive units are plainly closely related: a strong argument for reducing this character from its erstwhile subfamily rank to generic rank. Manter & Prince (1953: 110) found at the extreme posterior end of the body, a single clamp-sucker, half the size of the large kind and twice the size of the smaller. This may be the first-formed larval clamp, but no remnant of the protohaptor has been seen, yet larval anchors are reported for all other members of the subfamily.

The genital atrium is unarmed, though it is strongly muscular and the penis is protruded through it in an anterior-posterior direction, a very unusual orientation. Manter & Prince correct Linton's interpretation of the spiny penis : they consider it in relation to the laterally thorned penis of *Megamicrocotyle*, but it appears to me only remotely similar. In *Lintaxine cokeri* the ventro-lateral arc of penis-thorns are bent outwards, and dorsally there are graded needle-like knobbed spines, the shorter laterals of this set are provided externally with minute comb-like teeth. The median dorsal vaginal pore is unarmed, and lies mid-way between the atrium and the top of the ovary.



TEXT-FIG. 6. A-G *Diagram indicating the different lines of evolution of the "open sucker-clamp" in Microcotyloidea and Gastrocotyloidea :*

A. Typical, unmodified microcotylid clamp; B. Clamp-jaws have opened 'like a box', as in *Megamicrocotyle chirocentrus,* Tripathi 1956, smaller clamps, and in the larger clamps of Tripathi's "*Diplasiocotyle*" *chorinemi* and *Dicotyle stromatiei*; C. 'Fan-wise' opening of the clamps of the sessile row from *Heteromicrocotyla carangis,* Yamaguti 1953; D. Clamp-jaws have opened 'like a book', the dorsal jaw-rami and oblique braces having been jettisoned from the sucker-frame, as in *Thoracocotyle* spp. and in which the capsule-wall is strengthened by curved ribs; E. Similar 'book-like' opening of the clamp-jaws, the ventral jaw rami alone forming the sucker-frame, but there is no rib-like thickening of the capsule wall—the larger clamp-type from *Amphipolycotylochloroscombrus,* Hargis 1957; F. The clamp has 'opened like a book', but the dorsal jaw rami lie laterally while the oblique braces lie distally, neither contributing to the frame of the sucker—from one of the larger clamps of *Lintaxine cokeri* (Linton 1940) Sproston 1946 (from Manter & Prince 1953). In all, the ventral jaws and oblique braces are shaded black; G. Typical, unmodified gastrocotylid clamp.

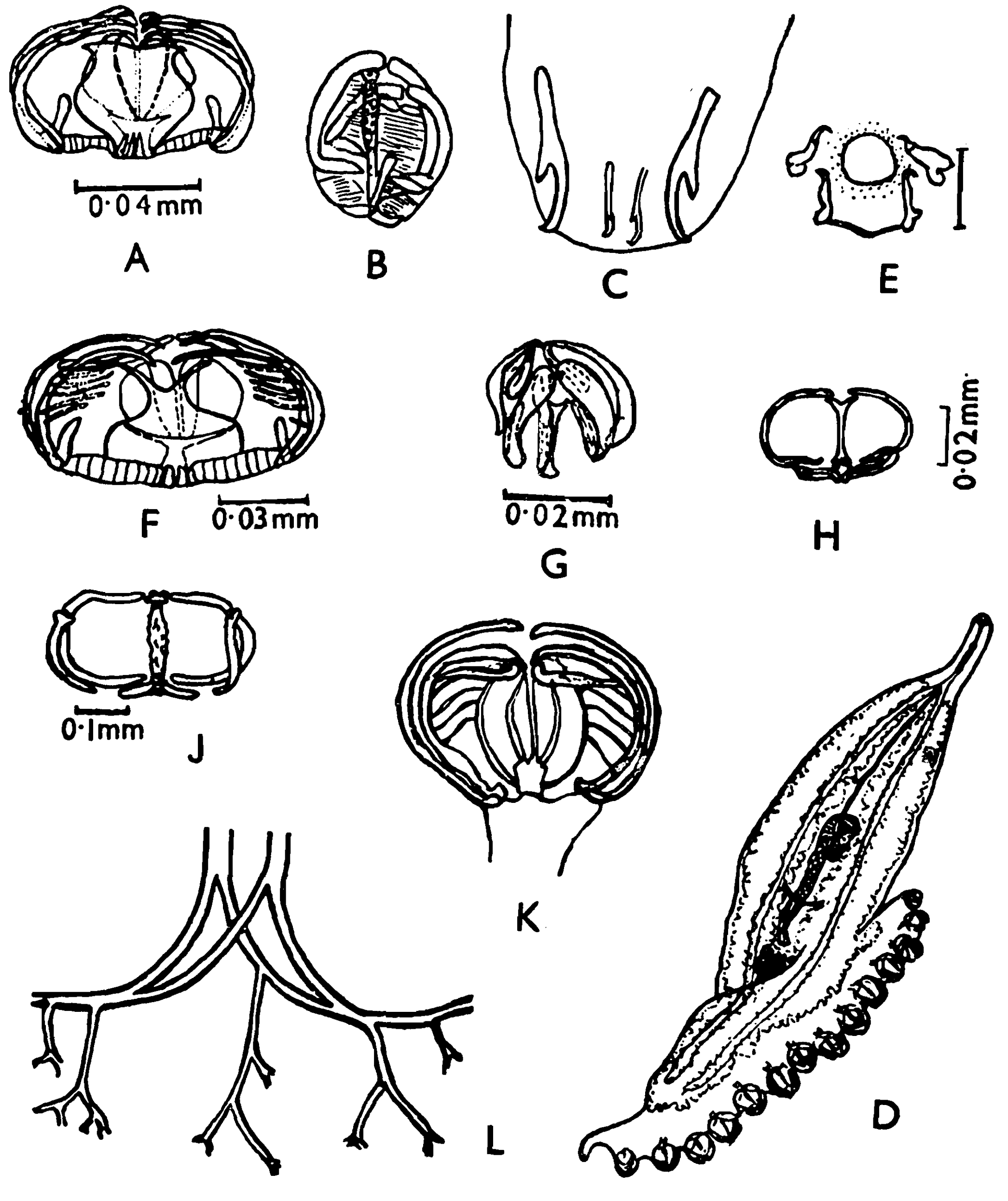
It is remarkable that so far this is the only Gastrocotyloidea species found on a Sciaenid fish (the euryhaline Sciaenid, *Pama pama,* yielded *Microcotyle pamae* Tripathi, 1956, in the Calcutta river).

Amphipolycotyle Hargis, 1957) : monotypic, with *A. chloroscombrus* Hargis (1957 : xiii : 2-3, figs. 1-6), on *Chloroscombrus chrysurus* (L.), a carangid from Florida waters.

The haptor is asymmetrical due to both qualitative and highly complex quantitative difference in growth stimuli in the two lateral longitudinal axes. Its resemblance to *Heteraxininae* is at once denied, not only by the unilateral modification of the clamps to the open-sucker type, but by the asymmetry being due to intervention of (unilateral) stimuli, and not the result of inhibitory influences which characterize Axinidae. At this moment it is pertinent to remember that in Heteraxininae any proximal diminution in size of the clamps is gradual, as in *Heteraxine heterocerca* (Goto), *H. chinensis* (Yamaguti), *H. karavoli* Unnithan, 1957 and *Crotalaxine serpentina* Unnithan, 1957, the result of a gradually increasing inhibition in the advancing growth-axis. But in *Amphicotyle* and *Tripathiana* (and perhaps in *Cemocotyle*) all forms with a unilateral flange-extension with atypical clamps, and suspected of being a metahaptor, there is an abrupt decrease in size for the 4 equal clamps at the anterior end of the row. In the bilateral metahaptor of *Thoracocotyle* spp. the change in size of clamps is also abrupt. In *Amphipolycotyle* the flange with sucker-clamps, adherent to the body proper up to mid-ovarian zone, may be part euhaptor and part metahaptor, while the short stalked more normal clamps on the other side probably represent only the euhaptor of that side.

The protohaptor is on a stout stalk and bears the 3 dissimilar pairs of larval hooks (the two pairs of anchors and the posterior pair of hooklets — *see* Llewellyn's generalized diagrams, 1957 a, fig. 5 *a, b*). The posterior 2 pairs of clamps are small, equal, open-sucker type whence, on the short side, no other sucker-clamps occur. On the long side they are all sucker-type, and the anterior 4 are abruptly smaller than the 8 which follow them. It may be then, that these are the missing 4 (2 + 2) from the anterior part of the larval haptor, have been pushed forwards to the end of the metahaptor by intercallary growth from a more posterior formative zone (as in *Thoracocotyle*) near the end of the body proper. In *Amphipolycotyle* this dual zone may be near the small clamp-sucker., No. 4 from the posterior end. This would indicate a very high growth-rate for the metahaptor, and a greatly depressed one for the euhaptor of that side. Moreover, the assumption is that the split in the formative zone in the larval haptor took place between the middle clamps, and the torque of the body axis, even in the larva, pulled the 2 anterior pairs of clamps from short side over to the metahaptor side and the 4 were carried forward in the metahaptor.

On the short side the clamps, after the first 2 sucker-type (*vide* Hargis: 1957, fig. 1) are all similar in shape and size, as in a regular euhaptor: it is a simple marginal nearly straight row., but only up to the hind end of the ovarian zone. These only slightly modified gastrocotylid clamps are, however, unique (Text-fig. 7, G): the jaws are markedly unequal, but the shorter ventral jaw rami twice as thick as the dorsal with broadly rounded ends, though their bent shoulder parts are normal. There is no appreciable internal asymmetry. As is so frequently found in gastrocotylid clamps (in contrast to microcotylid) the dorsal arm of the median spring is longer and wider than the ventral arm, and it is deeply cleft at the end, but lacks accessory sclerites in this or any other region. The open-sucker clamps, at least double the size, are like those in *Lintaxine* in lacking wall-ribs and having a simple oval frame made from the, now "C"-shaped, ventral jaw rami: the jettisoned dorsal jaw rami have slipped round under the posterior rim, just outside the oblique braces, here no longer articulating with the end of the spring (Text-fig. 7, H). The latter sclerites are in the same



TEXT-FIG. 7. A. *Pseudaxine mexicana*, Meserve, clamp ventral view (from Hargis, 1956); 26-28. *Pseudaxine vagans* Ishii. B. Clamp, C. Protohaptor with 2 pairs of anchors; D. Whole worm, dorsal view (all from Ishii, 1936); E. *Scombercotyle scomberomori* (Koratha 1956), dactylogyrid-like hooks round vaginal pore, and F. Ventral view of clamp (both from Hargis, 1956); G. *Amphipolycoryle chloroscombrus*, ventral view of small clamp, and H. Large-type clamp of open sucker row (both from Hargis 1957); J. *Lintaxine cokeri* (Linton), the larger open-sucker type of clamp (from Manter & Prince 1953); K. *Pricea minimae*, Chauhan 1945, pedunculated clamp, typical of the genus (from Chauhan); L. *Hargisiella hippos* (Hargis)—diagram to show the diamond-shaped circulus formed by branches of the intestine at the junction of the trunk with the euhaptor (to the left, posteriorly) and the matahaptor (to the right, anteriorly)—adapted from Hargis 1956 (x) fig. 19).

relative positions as they are in *Thoracocotyle,* the *Amphipolycotyle* sucker-clamps forming an evolutionary link with these and *Lintaxine* sucker-clamps.

Amphipolycotyle chloroscombrus is unique in the family in having consolidated testes : in two unequal elongated parts, the anterior (exceptionally) parovarial. This condition of the testes and the unusually posterior position of the ovary could be correlated with the torque tawards the stronger sucker-clamp (metahaptor) row from the early life. In *Vallisiopsis,* a similar torque, though more violent but from similar origins, has pulled the ovary and testes far back into the hind body and compressed them into the same zone. This effect is not seen elsewhere, either because the torque occurs in a flexible region (haptor-stem in Pyragraphorinae and *Pricea,* neck-region in *Thoracocotyle crocea*)., or when it occurs in the body region, the clamps on either side are not of markedly contrasting power and usually not attached to the body proper as they are here.

There is a muscular penis and the corona of typical erect spines is attached to the walls of the muscular atrium. The base of these hook-like spines is unusual in bearing a few outwardly pointing very short spines. A vagina was not seen.

Though the growth-rhythms are so very different in *Thoracocotyle, Dawesia, Lintaxine* and *Amphipolycotyle,* they are unquestionably related in respect of their clamp-type (*cf.* Text-figs. 6D-G).

PRICEINAE Chauhan, 1953, *s. str., emend.*

The subfamily as originally defined, on the basis of rib-like thickenings in the capsule wall, was heterogeneous regarding more fundamental clamp structure, and it embraced both the subfamilies, Thoracocotylinae and Gotocotylinae but the name and type genus may be retained for the new grouping based on different criteria. The clamps are basically gastrocotylid and are mostly symmetrical internally (Text-figs. 7A, B, F & K). Short ribs may be developed in the capsule wall, or not (a species character in *Pseudaxine*); but lamellae arising from the dorsal arm of the median spring, and the sides of the tendon-hole in the dorsal wall of the capsule, are developed as vertiable sclerites. In *Pricea* they support the inner ends of the lateral row of ribs forming the wide arched roof of the capsule, in *Pseudaxine* they do not reach the ribs but are still wide, and in *Neothoracocotyle* they are much narrower or incipient (lightly cuticularized and probably overlooked (?) in *N. coryphaenae* Yamaguti). The bulbous penis is remarkably uniform in all species, with a similar number of spines in the corona. This, however, may well be the muscular wall of the *atrium masculinum,* partly protrusible as a grapple, with an unarmed simple, more or less muscular, penis emergent within it, as shown in *Amphipolycotyle* (Hargis, 1957: xiii, fig. 2). In *Scomberocotyle* the bulbous penis is exceptional in having a crown of long spines like needles emerging through a long-spined atrium. The single dorsal vagina, where known, is unarmed and without accessory suckers or armature, except for the unique dactylogyrid anchor complex round the dorsal vagina of *Scomberocotyle* (Text-fig. 7, E).

The growth-rhythms in the haptor of Priceinae show even more variety than in the last two subfamilies: complete inhibition of growth in the one lateral longitudinal axis (*Pseudaxine*), combined with secondary stimulation on the other, leading to the formation of a unilateral metahaptor in *Pseudaxine*, a simpler unilateral metahaptor in *Scomberocotyle;* and a bilateral metahaptor, of protohaptoral origin, in *Pricea;* while in *Neothoracacatyle*, where the haptor/body-axis has been suppressed (as in *Pseudaxine*), there is a high growth potential in both lateral longitudinal axes of the haptor, resulting in a simple euhaptoral frill on each side of the body for more than half the total length. The four genera included in *Priceinae* emend. nov. are: *Pricea* Chauhan, *Neothoracocotyle* Hargis (2 spp.), *Scomberocotyle* Hargis (1 sp.), and *Pseudaxine* Par. & Per. (4 spp.)

Pricea Chauhan, 1945: has the most highly developed haptor of the sub-family, showing every sign of high growth potentials operating without inhabitory influences,, and there is both internal and external symmetry: the body as a whole develops a transient asymmetry due to postural causes. There is a more or less long metahaptor, its pedunculated clamps continuous with those of the lateral rows on the euhaptor. Recognisable primary, larval clamps have not been recorded, but a single pair of unique larval anchors occur on the posterior rather wide lappet: these have split ends producing two subequal points, *analogous* to certain Dactylogyrid anchors (*Falciunguis* Achmerov 1952, shows the beginning of this tendency): Bychowsky (1957 fig. 312), compares the *Pricea anchors* with those of *Dactylogyrus pterocleidus* Gussev, and *Urocleidus acer Mueller.* There is a second pair of larval anchors, termed "body hooks" by Chauhan and Ramalingam who have both contributed species to *Pricea*: these are usually squat stout hooks with short wide bifid roots and a sharply reflexed point, and they are said to be situated in varying positions on the haptor axis, but usually near the origin of the metahaptor ; that is, where the clamp frills leave euhaptor-body axis to form an independent (morphologically ventral) lobe growing anteriorly.

This fact is an additional proof of the dichotomy of the haptor axis early in life, but in *Pricea,* the dichotomy evidently took place in the protohaptor, infact between the two principal pairs of hooks (anchors), producing a double formative zone : one replicating clamp on the anterior side and the other on the posterior side. The result would be to force the anchor-pairs increasingly farther apart ; but the proximal anchors, being associated with muscles attached to the wall of the body-proper, would be torn away from the anterior tip of the new metahaptor, as it budded off from the body-euhaptor axis to form an independent outgrowth. The metahaptor may then be assumed to retain its formative region immediately anterior to (the morphologically proximal end of) the euhaptor. The anterior side growth is not accelerated to such an extent as the posterior, fòr the metahaptor is seldom as long as the euhaptor, particularly in the smaller "species" named, though in the largest (*P. multae* Chauhan and *P robusta* Ramalingam) the metahaptor is nearly as long as the euhaptor.

In its natural position on the gill-filaments, the body is bent, as usual, at rightangles and then obliquely laterally to the haptor axis, so that in the detached worm the appearance is of an inverted "T". In the instances where the "body-hooks" are depicted some way down the metahaptor they are probably seen through its thickness, and are actually *in situ* on the posterior end of the body proper, as in Chauhan's figures in his first (1945) paper. In view of these considerations it is most probable that Ramalingam's species will prove identical with one or more of Chauhan's. The loss of one or more of the "body-hooks" or their displacement as a result of operative trauma may be expected.

Another manifestation of high growth potentials in the longitudinal axes of both the euhaptor and metahaptor, is the doubling of the marginal rows of clamps figured in most of the "species" This means that in the formative zone, in addition to the primary and persistent dichotomy of the axes (anterior and posterior juxtaposed zones of replication), there is a secondary lateral dichotomy of each of the 4 axes. But this may be spasmodic: sometimes both sides of either euhaptor or metahaptor may have double rows for a short distance, then resume the double row, or one side only may be double for a varied distance. This doubling of the rows of clamps has already been noted for *Chauhanea.* The same lateral replication at the same time as the serial replication of clamps, is known to occur in *Gotocotyla* spp. from *Scomberomorus* spp. in India, and it has been indicated in the proximal region of *Gotocotyla elagatis* Meserve (1938, fig. 37), similarly in *Lithidiocotyle secunda* Tripathi (1956, fig. 2*f*). It may not be uncommon in *Microcotylinae,* but until recently we have interpreted figures of 'over-crowded clamps' as being due to contraction and mere overlapping: this is certainly not so in the above examples, and *Microcotyle priacanthi* Meserve (1938, fig. 30) with mostly about 7 clamps abreast in the proxinal half of the haptor, should be looked upon with a new interest.

The clamps of *Pricea* spp. are remarkably uniform and symmetrical according to the figures (Text-fig. 7K): the ventral jaw rami just fit over the dorsal jaw rami like the lid of an oval box, except anteriorly where the oblique braces are fitted between them when the capsule is closed. The ventral arm of the spring is narrow and not forked at the end, but the dorsal arm, though short, has two broad tapering lamellae supporting the 5-7 ray-like ribs under the roof of the capsule, which appear to articulate laterally with the dorsal jaw rami. The clamp pedicels are highly mobile and contractile: they may owe their varying diameter to turgor provided by a water-vascular system homologous with that referred to in Opisthogyninae, and already described for some Axinidae (Unnithan, 1957). This is suggested by the slender flaccid peduncles of some and the thick or bulbous peduncles of others in Chauhan's (1945, fig. 37) carefully drawn figure and also by the exceptionally wide extension of the lateral excretory ducts in the hind body. The peduncles in *Pricea* are only sparsely muscular.

The vagina is just over the intestinal bifurcation and its opening sac is claimed by Chauhan (1945) to have a "U"-shaped spring within it and a sucker-like 'vulva', usually triangular; but some of the figures suggest that the spring or U-hook in the vaginal sac may be an optical effect of a thick cuticular lining; but cuticular structures were lacking in three of Ramalingam's species.

Genotype: *Pricea multae* Chauhan, 1945, on *Cybium* (?) *lineolatum* Cuv., from Bombay (Arabian Sea); *P. minimae* Chauhan, 1945 on *Katswonus pelamys* (L.), from Bombay; *P. microcotlae* Chauhan, 1945 on *Rastrelliger kanagurta* (Russel), from Bombay; *P. tetracantha* Ramalingam, 1952 on *Cybium guttatum* Cuv., from Madras (Southern sector Bay of Bengal); *P. armata* Ramalingam 1952, on *C. guttatum* Cuv., from Madras, and the same host and locality for the following species; *P. tricantha* Ramalingam, 1952; *P. melane* Ramalingam 1952; *P. minuta* Ramalingam 1952; and *P. robusta* Ramalingam 1952.

Neothoracacatyle Hargis 1956: erected for two closely related species formerly in other genera, on the basis of similarity of their modified gastrocotylid clamps, which are not open suckers as in *Thoracocotyle* MacCallum. Genotype: *N. coryphaenae* (Yamaguti, 1938 -as *Thoracocotyle*) on *Coryphaena hippurus* L. from the Japanese Pacific; and the second species *N. acanthocybii* (Meserve 1938 — as *Gotocotyla*) Hargis 1956 on *Acanthocybium solandri* Cuv., from the Galapagos Islands.

In *Neothoracocotyle* the haptor/body relationships are similar to those in *Thoracocotyle,* except that there is no metahaptor, for after the protohaptor there is no growth in the haptor-body axis, though the longitudinal axes of the haptor have a high growth potential, so that they grow forwards as lateral flanges adherent to the sides of the body past the ovarian zone. This far anterior extent of the haptoral flanges is otherwise rarely found, but another instance is in *Prosomicrocotyla gotoi* (Yamaguti 1934) Yamaguti, 1958 (*Microcotylidae*)—a character on which Yamaguti (1958, liii: 83) erected this genus, with *Microcotyle chiri* Goto 1894, as the second species, both on *Hexagrammos otakii* Jord. & Starks.

The clamps are all alike in size and shape and are internally symmetrical, but they differ from those of *Gastrocotyle* in that the short dorsal arm of the median spring bears a pair of lamellar sclerites, homologous with those in *Pricea* and the next two genera, but here much narrower and not reaching the roof-ribs. They clearly act in strengthening the sides of the tendon-hole (incipient cuticularization' shown' by Subhaprada in *Gastrocotyle indica*), as well as supporting the capsule roof. Unfortunately Yamaguti omitted the dorsal arm of the spring entirely from his figure of *N. coryphaenae,* but Hargis' reinvestigation of the type material of *N. acanthocybii* (Meserve) Hargis (1956, xii: fig. 25) has established this generic character. There are 4 pairs of straight, not very long, parallel ribs developed in the dorsal capsule wall in both species. The protohaptor is represented in the adults by one pair of rather long-handled sickle-hooks.

Both species grow to the great length of 11-12 mm. and the haptor extends for a little more than half that length, but in *N. coryphaenae* the whole gonad zone is in the posterior fourth of the worm; the ovary is shorter, and the numerous testes are in two very regular parallel ranks. The wide oval genital atrium is armed with several hundreds of long-rooted slender spines; there is probably an unarmed penis (not an armed cirrus as Hargis's figure-caption suggests, since both original authors describe only the atrium as armed and the vas deferens opening into it). The vagina opens at the posterion fourth of the anterior vitellaria-free zone which is about one-seventh of the total length in the genotype but one-fifth in *N. acanthocybii.* The vaginal pore is in a wide transverse oval of muscular tissue middorsally. The vitellaria begin with the crural branches and extend nearly to the end of the body, a little infront of them here, the crura become confluent. The oval oral suckers are aseptate. Several 2-filamented eggs may occur in single file in the uterus.

Scomberocotyle Hargis 1956 — erected for *Heteraxine scomberomori* Koratha (1955) found by both authors on *Scomberomorus maculatus* (Mitchill) and *S. cavalla* (Cuv.), from Florida and Texas coasts. No other species. Elongate slender priceine worms with an asymmetrically developed haptor and probably a unilateral metahaptor. Hargis (1956: xii, fig. 2) shows that the longer clamp row with its anterior flange has caused the posterior end to be deflected to the opposite side, as in *Heretaxine.* The protohaptor is represented by a stout terminal lobe bearing a single pair of anchors with roots barely as long as the long sickle-shaped hooks; moreover on the proximal end of each there is a conspicuous ampoule-like structure (gland reservoir ?) frequently seen in Dactylogyridae, but exceptional for Discocotylinea.

The clamps are all alike, but in the two rows distal to the lobe they are in not quite equal numbers: those on the straight side being more crowded, and both rows (here considered as the euhaptor) are equally long. There is an increase in clamp-size towards the middle, and a marked diminution at the proximal end of the straight row. The curved and slightly irregular edge of the other side shows that the increased clamp-size to the middle is maintained to the end, where there is an abruptly projecting wide lobe-like flange and a gap in the clamp-row, which is then continued round the slight curve of the flange, (which is considered to be a metahaptor). About one-third from the anterior end of the metahaptor there is a marked diminution in size of a few of the clamps, and opposite to this is an unusually long branch from the intestinal crus, accompanied by a few vitelline follicles outside their otherwise limited field. It suggests that this may be the formative zone of the metahaptor, and by analogy with *Pricea,* a second pair of larval anchors might be found here. This is an hypothesis which the American colleagues will be able to test and modify. The asymmetry is therefore due to growth-stimulation, rather than to inhibition as in *Heteraxine.*

Another peculiarity in *Scomberocotyle* is the presence of accessory buccal suckers, close against the large septate suckers with the opening tilted opposite to the septum, but quite independent from the normal sucker. The only similar condition is in *Diplozoon nipponicum* Goto, 1891.

The genital atrium has a dense double rosette of straight spines with bent tips and the muscular penis, as usual globose with a spiny corona, but here the penis-spines are needle-like. The vaginal pore is similarly situated to that in *Neothoracocotyle,* but it is unique in having on its flanks two pairs of hooks strongly reminiscent of dactylogyrid anchors. The anterior pair have broad bifid roots and separated sharp points, and the posterior, similar but more slender, are connected by two narrow bars (!). The proximal parts of the vagina are not indicated.

Pseudaxine Parona & Perugia 1890, contains at least 4 species which vary mainly in the extent of the unilateral haptoral flange along the one side of the body, from which it may be free distally. The genus shares with *Gastrocotyle* the unusual character of the complete inhibition of the haptor on one side, but *Pseudaxine* differs mainly in the euhaptor being oblique and not parallel to the body-axis, and not extending to the ovarian zone; in particular, in those species which have been more recently re-examined, additional sclerites have been found associated with the dorsal arm of the spring. The genus still needs re-investigation, especially in respect of the armature of the genital atrium figured only for the genotype from the Mediterranean, and also of formative region for the clamps near the middle of the row, and the structure of the dorsal region of the clamps themselves.

In *P. trachuri* Par. & Per., there is a brief gap in the clamp-row opposite to the intrusion of a branch from the intestine into the flange (Sproston 1946, fig. 109 *a*); and in *P. mexicana* Meserve (1938, fig. 60), there is an abrupt diminution in size of 2 clamps, just proximally to the middle of the row and opposite to the level at which the flange becomes free from the body. Both these instances of interruption in the clamp succession suggest the occurrence of a formative region: in other words, that the proximal, partly projecting sector of the row, is in fact *a metahaptor.* The single smaller clamp found in both these species on the proximal tip of the haptor would then be the first-formed clamp of the metahaptor, and not a recently formed clamp as originally suggested by Sproston (1946: 465). So that both in *Scomberocotyle* and in *Pseudaxine* there is the possibility of a unilateral metahaptor, but nothing of the kind occurs in the apparently similar *Gastrocotyle* spp. There is also a slight diminution in size of two adjacent clamps in the middle of the haptor in *P. vagans* Ishii (1936, fig. 9), and certainly a smaller clamp at the tip; the last 3 clamps being on the free part of the flange which here extends exceptionally far along the body to the distal end of the ovarian zone, where a fold on the opposite side of this widest region. causes a somatic asymmetry faintly resembling that in *Thoracocotyle ovalis* Tripathi.

The clamps in *P. trachuri* and *P. vagans* are about as long as wide, in *P indicana* slightly wider, and in *P. mexicana* about twice as wide as long. The latter, recently restudied by Hargis from new material from Florida (1956, xii, fig. 1) shows an immensely expanded ventral arm of the spring (escutcheon-shaped) and widely bifurcate anteriorly, while the short dorsal arm bears two triangular plates, very similar to those in *Scomberocotyle scomberomori.* In the Pacific material of *P. mexicana* the accessory dorsal plates are shown much narrower

(Meserve 1938, fig. 61), and there are 6 or 7 oblique ribs, absent from the Florida specimens (Text-fig. 7A). In *P. trachuri* ribs are also absent and the dorsal accessory sclerites are short, as they are in *P. indicana* Chauhan (1945, fig. 20), and the jaws are as stout as they are in *P. vagans* Ishii (1936, fig. 10, Text-fig. 7B). In both the last two species the spring is stout and is associated with two cuticularized horns apparently supporting the anterior edge (hinge) of the capsule: Ishii does not indicate any dorsal accessory sclerites. All authors agree that there are two dissimilar pairs of anchors on a projecting lappet (protohaptor) and that the penis has a corona of nearly straight spines (10-22), but none could see a dorsal vagina: the lateral paraoesophageal vaginae referred to by Ishii may after all not be excretory vesicles or pores.

Genotype: *Pseudaxine trachuri* Par. & Per., 1890, on *Trachurus trachurus* (L.) from the Mediterranean, English Channel, and two localities in Japan (in the last three localities found in association with *Gastrocotyle trachuri*); other species:—*P. vagans* Ishii, 1936 (Text-fig. 7D) on *Katsuwonus vagans* (Lesson), from Japan ; *P. mexicana* Meserve, 1938 on *Scomberomorus maculatus* (Mitchill) and *S. cavalla* (Cuv.) from the Mexican Pacific, and from Florida; (Hargis 1956 considers that *P. texana* Koratha 1955 from the same hosts off Texas is synonymous with *P. mexicana*); *P. indicana* Chauhan, 1945 on *Sparus berda* Forsk., from Bombay (Arabian Sea); and *P. kurra* Unnithan, 1968 on *Caranx kurra* Cuv. & Val. in association with *Gastrocotyle kura* Unnithan, 1968 from Trivandrum, Arabian Sea.

ENGRAULICOLINAE Subfam. nov.

The new subfamily has been created to accommodate *Engraulicola* George, 1960 and allied genera of atypical gastrocotylid worms in which the tendency to unilateral inhibition of the clamp rows is incomplete, resulting in a long and an opposite short row of gastrocotylid clamps. The short row is represented by a minimum of one primary clamp (as in *Engraulicola* George, 1960) and may extend to half or nearly half the number and/or length of the long clamp row in some genera (as in *Pellonicola* Unnithan, 1967). The structure of the clamp in the short and long row is similar and essentially gastrocotylid. It is interesting to note that the short clamp row which has been retained as a result of incomplete inhibition occupies the euhaptoral area just in front of the protohaptor. Beyond the distal level of the euhaptoral frill of the short clamp row the haptor continues forward on the long clamp row side as a unilateral metahaptoral frill which is indicated by the posterior level of haptoral extensions of body organs. The subfamily may reflect an indirect parallel condition in Heteraxininae of Axinidae Unnithan, 1957. However, in Engraulicolinae the condition of the haptor is the result of a tendency to incomplete unilateral inhibition of the clamp rows. Type genus: *Engraulicola* George, 1960.

Other genera included in the subfamily are *Engraulixenus* Unnithan, 1957 (1 sp); *Engrauliphila* Unnithan, 1967 (1 sp); *Engrauliscobina* gen. nov. (2 spp) and *Pellonicola* Unnithan, 1967

(1 sp). (cf. Unnithan, 1967 for detailed description of the species included under these genera).

Engraulicola George, 1960. A detailed description of the genotype *E. forcepopenis* recorded on the gills of the Indian clupeoid fish *Anchoviella bataviensis* (Hordenberg) at Trivandrum (Arabian Sea) has been given by George (1960).

Engraulicola micropharyngella Unnithan, 1967 — the second species of the genus was collected from the gills of *Anchoviella commersonii* (Lacepe) also at Trivandrum (Arabian Sea). Relationship of *E. micropharyngella* has been fully discussed elsewhere (cf. Unnithan, 1967).

Engraulixenus Unnithan, 1967: Monotypic with *Engraulixenus malabaricus* from the gills of *Thrissocles malabaricus* (Bloch) at Trivandrum (Arabian Sea). Has an elongate tapering body, slender anteriorly, with long foot-shaped hindbody tapering backwards and which has an unusually prominent heal with a spurlike extension forming the metahaptor. The inhibited clamp row retains two clamps of similar structure though smaller in size than those on the long clamp frill, the dorsal appendix of the median spring is a stalked 'U'-piece with parallel arms not divergent as in most of its relatives. The ventral arm of the spring is not truly bifurcated and is slender throughout. The anterior anchors have a characteristic shape — with handle markedly longer than the hook which is bearly one quarter of a circle and with a stepped concial spur at right angles to the handle. Paired vaginae and exceptional intercrural bridges are present and the crural ends are subequal and markedly inflated. Parasitic on marine fishes.

Engrauliphila Unnithan, 1967: Another monotypic genus. The genotype *E. grex* was collected from the gills of *Thrissocles dussumieri* (Val.) at Trivandrum and Ayirumthengu (Arabian Sea). Those from Trivandrum had a closely related species *Engrauliscobina triaptella* Unnithan, 1967 also on the same host specimen. *Engrauliphela* has haptor-body relation similar to that in *Engraulixenus*. The inhibited clamp row retains two primary clamps only. The two pairs of persistent anchors are characteristic, both less curved than in *Engraulixenus* and entirely unlike those of *Engraulicola*. The penis head is devoid of forceps and a collar is lacking round the atrium. Paired lateral vaginae join tranverse vitelline ducts, the vulvae are not supra-marginal and they are situated much nearer to ovary. Pharynx is elongated ovoid. Parasitic on marine fishes at a very high infection rate.

Engrauliscobina gen. n. has been erected for *Gastrocotyle thrisocles* Tripathi (1959 : 124-5, fig. 56) found on *Thrissocles mystax* at Puri, in the northern sector of the Bay of Bengal. This species is excluded from *Gastrocotyle* v. Ben. & Hesse, by its triangular body and the incomplete suppression of the clamp row on the longer side of the body. In *Gastrocotyle* there is a complete suppression of haptoral growth on the one side, and the clamps on the other, always parallel, side of the body extend as a rule well above the gonad zone.

Its peculiar shape suggested its new name (*Engraulis* — the name of the type genus of the hostfamily., and *scobina* — Latin for a rasp, or scraping tool): a shape resembling that of *Pseudaxine vagans* Ishii, in which the oblique haptor also extends about half way up an exceptionally wide body; but again, there is a complete inhibition of the other side of the haptor. The finger-like protohaptor is very like that in *Pseudaxine indicana* Chauhan, in that the proximal pair of larval anchors are far separated from the posterior pair. Here they are set transversely on the blunt end, with a minute pair of larval hooklets between them. The posterior anchors have very short bifid roots, while the penultimate pair are thrice the length and the straight root is longer than the elongated sickle.

In the retention of two small token clamps on the inhibited side, *Engrauliscobina* gen, n. is analogous to *Axinoa aberrans* (Goto, which has only a single token clamp. There is no information published either on the detailed structure of the vestigial clamps (Tripathi's 1959, Fig. 56 *c*) or on that of the larger clamps crowded in profile view along the main row, but their oblong shape suggests a possible modification of their basic gastrocotylid sclerites (cf. George, 1960). The brevity of Tripathi's description is partly compensated by his figure, which shows that while there is no exact counterpart of the minute rounded token clamps on the opposite side of the protohaptor, the first two (primary) clamps are already elongated, but much smaller than the others except for two similar (primary) clamps at the far anterior end of the row, on a short lobe projecting from the body margin. Moreover., in the middle of the clamp-row there are two small clamps flanked by two of medium size, all slightly indented towards the boundary of the body proper. This region suggests the site of the formative zone: backwards for the euhaptor, and forwards for the metahaptor, which has carried the last two primary clamps of that side away on its advancing tip. The dichotomy of the growth-zone in the larval haptor would thus have taken place between the middle pairs of primary clamps, producing secondary replications on either side of the zone on the one flank, while there was a complete suppression of the growth zone and the clamps of the larval haptor anterior to this level on the other flank. In *Pseudaxine* there was evidently a complete inhibition of primary clamps on the larval haptor on this flank, and the dichotomy of the formative zone for secondary clamps took place between the two anterior of the four primary clamps on the uninhibited flank: since in *Pseudaxine* spp. there is but a single diminutive clamp on the anterior tip of the metahaptor.

In *Engrauliscobina thrissocles* and its allies, the whole of the body just behind the genital pore is packed with rather large vitelline follicles which obscure most of the internal organs, so a vagina has not been detected in any of them: in addition, since they are blood-feeders from the gill-tissue, melanotic granules deposited on the walls of the richly branched intestine add to the obfuscation. The anterior quarter of the long side (hypotenuse of the rightangled triangle) of the worm forms a narrow cylindrical 'handle of the scraper', and the genital pore is at about one-third its length from the anterior end. The bulbous atrium masculinum carries a corona of 12 erect hooks just as in *Pseudaxine mexicana* (about double this number in *P. vagans* and *P. indicana*).

The undoubted affinity of *Engrauliscobina* with *Pseudaxine* and *Gastrocotyle* raises a phylongenetic problem, since the last two are so characteristic of Carangid and Scombroid fishes, but the new genus is parasitic on the relatively primitive *Engraulidae*. It is a precisely parallel problem to that posed by the distribution of the Mazocraeid genera *Kuhnia* (on *Scombridae*) and *Mazocraes* (on *Clupeidae*): a question discussed by Bychowsky (1957:307, and schemata in figs. 263, 264, 265).

Engrauliscobina triaptella Unnithan, 1967: This species was obtained from the gills of *Thrissocles dussumieri* (Val.) at Vizhingam, Trivandrum (Arabian Sea). The host specimen examined at Trivandrum had multiple infection by *Engrauliphyla grex* Unnithan also. In *E. triaptella* the clamp flange is 36% to 48% of the total length while it is 50% in the genotype and there are 3 remnant clamps on the inhibited side of the haptor of this species. The number and extent of the clamps and its frill in the two species differ considerably. In the structure of the clamps and anchors also there are specific differences. Internal organs also show specific variation in the two species of *Engrauliscobina* as detailed in Unnithan (1967).

Pellonicola Unnithan, 1967: Monotypic with *P. elongata* Unnithan, 1967 obtained from the gills of *Pellona* (*Ilisha*) *brachysoma* (Blkr.) at Trivandrum (Arabian Sea). Body elongate ribbon like with distinct but short caudal haptor. The unilateral inhibition is far less than in any other genus of the subfamily and in this respect is comparable with *Scomberocotyle* Hargis, 1956 but in that genus a metahaptoral wing or secondary stimulation of secondary clamp replication accounts for the large number of clamps on one side. The anterior moiety of the long clamp row may on further observation prove to be a metahaptor and its posterior moiety being the euhaptor parallel with its counter part on the opposite side of short clamp row, the short row has nearly half the number of clamps in the long row. The two pairs of anchors are on a telescopic lappet. There are few parovarian testes though they are mainly postovarian. Penis corona has no additional sclerites and the paired vaginae are supra-marginal as in *Engraulixenus* but very far forwards. There is a median vitelline duct. Oral pouches are particularly large and better developed than in other genera. Parasitic on marine fishes.

GOTOCOTYLINAE Subfam. nov.

This subfamily of Gastrocotylidae is erected for what at present appears to be a single genus, *Gotocotyla* Ishii, 1936. Yet it stands in contrast to all other genera of the family in the extreme internal asymmetry of the clamps (Text-fig. 5A): on the one side the ribs from the capsule roof have been incorporated into the supporting skeleton of the side-wall and are often ankylosed to the ventral and dorsal jaw-rami of that side to form a ladder-like compound sclerite, while the ends of the rami are variously bent and hooked. On the wider side of the clamp the sclerites derived from the dorsal arm of the spring (simple lamellae in *Priceinae*) are variously shaped or even divided, and the shoulder-piece of the ventral jaw on this side is expanded and may be free. The median spring, elongated and slender, is variously bent away from the meridian and ends in a hook-like point anteriorly, but its dorsal arm is reduced. The oblique braces are unequally developed: that on the wide side always wider and longer. There is a symmetrical haptor as a continuation of the body-axis (its possible partition is discussed below), and the terminal hooks of the protohaptor are retained in the adult.

These species are also exceptional in this family in having a long eversible true cirrus, bearing hundreds of sharp spines, or according to Hargis (1956, fig. 15) long-handled hooks with short points. There is a conspicuous dorsal vagina, usually surrounded by a wide rim of circular muscles and sometimes gland cells.

It is noteworthy that all but two (one doubtful) records are from hosts belonging to either Scomberomoridae (=Cybiidae auct.) or Scombridae.

Gotocotyla Ishii (1936 : 788) is apparently the only valid genus. Syn.: *Lithidiocotyle* Sproston, 1946, was created without a full understanding of Ishii's genotype, and as Tripathi has proposed (1959 : 129), the genera must be merged (unfortunately he suppresses *Gotocotyla* in favour of *Lithidiocotyle* in his Key on the next page). I also concur in his making *Pseudomicrocotyle* Sandars (1947) a second synonym. *Microcotyle (sensu lato auct.)* is also a synonym in part. The following notes do not purport to be specific diagnoses, but they draw attention to some possible specific criteria for this compact group, yet evoking so many problems.

Genotype: *G. sawara* Ishii, 1936, on *Cybium niphonium* Cuv., from Japan: numerous testes occupying at least half the length of the body, preceded by a large receptaculum seminis behind the proximal lobe of the inverted "U"-shaped ovary, and extending into the haptor; but the unbranched ends of the intestinal crura extend farther, nearly to mid-haptor level. There is a sclariform sclerite on the adaxial side of the clamp, and the shoulderpieces of the ventral jaw rami are atriculated hooks (Text-fig. 5A).

G. acanthura (Parona & Perugia 1896 — as *Microcotyle*) Meserve 1938 (Syn. *Lithidiocotyle acanthura* (Par. & Per.) Bychowsky (1957: 439) on *Brama rayii* (L.), from Genoa (Mediterranean), and North Sea.

G. lintoni nom. nov. pro *Microcotyle* sp. of Linton (1906: 370, figs. 147-150) on *Pamatomus saltatrix* (L.), from the American Atlantic: non *Microcotyle pomatomi* Goto, 1899, from the same host off Rhode Island USA, which Linton (1940) identified with his *Microcotyle* sp. of 1901, also from *Pomatomus saltatrix* — *M. pomatomi* has been re-studied and its ontogeny described by Bychowsky (1957 : 207-8, figs. 241-3) from the same host from the Black Sea. *G. lintoni* was said to have clamps twice as wide as long, and though the figure is admitted to be a crude sketch, the asymmetry is consistent in that the shoulder-piece is much longer on the wider side, and the oblique braces are conspicuous; the highly characteristic spiny cirrus is nicely figured, and here the sharp spines have bifid bases; the vitellaria occupy two-thirds of the body but do not enter the haptor, and the vaginal pore may be slightly lateral. These worms are unusually small: 2.3 to less than 4 mm. long, whereas both the foregoing species are at least 10 mm. long.

G. acanthophallus (MacCallum & MacCallum 1913 — as *Microcotyle*) comb. nov. (Syn. *Lithidiocotyle acanthophallus* of Sproston 1946 — genotype: and of subsequent authors), on *Roccus saxatilis* (Walb.) from Atlantic coast of USA. The type material has been re-examined by Hargis (1956, xii: 37, figs. 10, 11), and the terminal anchors figured for the first time; the 5 or 6 short ribs do not contribute to form a scalariform sclerite, and the shoulder piece of the ventral jaw on that (adaxial) side does form an articulated hook, there is a third (saddle-shaped) free dorsal sclerite proximally near the short end of the spring. The testes and vitellaria do not enter the rather long stem of the haptor, though unbranched crura do. The vaginal sucker is very wide: a transverse oval in the mid-dorsal line in the zone of the intestinal bifurcation. The MacCallums' worms were 7 mm. long.

Hargis considers the worms from *Scomberomorus cavalla* and *S. maculatus*, which he found in Florida waters to be conspecific with MacCallums' which he thinks may have been accidental passengers on *Roccus* from the fish-market. His worms from *S. cavalla* were larger and more numerous than those on *S. maculatus*, yet the clamps from the former are still smaller than those from *Roccus* according to Hargis' 1956: figs. 10 & 19), and so are the proximal (Penultimate) larval anchors, though similar shape, the handle forms a broad triangular sleeve for the 'C'-shaped hook. In the terminal anchors the 'C'-hook is relatively longer in the worms from *S. cavalla* than from *S. maculatus;* in the clamps of both the latter, the third free dorsal sclerite is not developed.

There may be a case here for the establishment of three subspecies, but the array of qualitative variation data for each needs amplification, particularly in view of Ramalingam's discovery of clamp polymorphism within the individual (see below).

Hargis attempts to retain this species in *Lithidiocotyle*, and redefines the two genera, but he admits the differences are very slight: the lateral extent of the testes over the crural fields and the relative length of the haptor-stem. I think he may agree after examining data from Indian material (Ramalingam 1961) that these differences are only of specific rank, and that *Lithidiocotyle* Sproston, is a clear synonym of *Gotocotyla* Ishii, 1936.

Hargis thinks it highly probable that *Microcotyle scomberomori* Koratha, 1955, from the Texas Coast on the same *Scomberomorus* spp., is a synonym of *G. acanthophallus.*

G. elagatis Meserve, 1938 (Syn. *G. elegatis* Mes. of Hargis, 1956, 28, 38, 39, 42), on *Elagatis bipinnularis* (Quoy & Gaimard), from

Bahia Honda, Panama (*Sic*): — this citation is ambiguous,, since Bahia Honda is in western Cuba, far from Panama; and though it is possible that the Galapagos-bound ship called at this coaling station, it is more likely to be one of the two ports named Bahia in Equador. "Bahia" opposite Quito and just south of Cape San Francisco would be among the nearest continental landfalls from Galapagos, and is suggested as a more probable locality. If it can be established that the origin of Meserves material is in Pacific waters, it is a further point in favour of Sandar's *Pseudomicrocotyle elagatis* from the same host species in southern Australian waters, being identical with Meserve's: resulting in the homonym *Gotocotyla elagatis* (Sandars 1947) comb. nov., but if the identity is valid, there is no need to substitute a new specific name for Sandars material.

Hargis has re-examined the type material (1956, xii, 39, figs. 20-23), and his more detailed figure of the elongated clamps (twice as long as wide) shows a scalariform compound sclerite on the adaxial side articulating with an expanded shoulder-piece,. There is probably only one free dorsal sclerite developed, the proximal lamella being the dorsal arm of the ventral jaw ramus of the abaxial side,. The hundreds of testes overlap the crural fields, and are flanked by vitellaria for only half their zone; feebly diverticulate ends of the crura extend half way down the haptor. The cirrus has long needle-like spines with a short rightangled bent at the bases. The terminal anchor hook is less than a semicircle. Hargis finds two lateral rows of clamps on one side, but Meserve figures three, in the proximal half of the haptor. The vagina is evidently inconspicuous since it is not mentioned by either author.

Gotocotyla meservei Yamaguti 1953 also occurs on *Elagatis* sp. but from the extreme western Pacific, off Celebes. It differs from *G. elagatis* Mes. in the significantly fewer testes, the shorter crura which reach only half way down the testicular zone, where the vitellaria also cease, and the male terminalia are said to be different. In the oval clamps there is an adaxial sclariform sclerite and one dorsal plate is very wide.

G. secunda (Tripathi, 1956 — as *Lithidiocotyle secundus*) comb. nov., occurs on *Scomberomorus guttatus* (Bl. & Schn.), from Puri, in the northern sector of the Bay of Bengal. It is claimed to differ on account of the presence of anchors, but these have now been found (2 pairs, one terminally and the other, smaller, in the anterior dorsal region of the haptor) on the former genotype by Hargis 1956. In *G. secunda,* however, the testes are in only 2 rows and the crura are said to enter the haptor; the oral suckers are relatively as well as absolutely much smaller and the muscular vaginal opening is longitudinally oval instead of transverse, it may also, be slightly lateral.

G. bivaginalis (Ramalingam, 1961 as *Lithidiocotyle bivaginalis*) comb. nov. on *Scomberomorus guttatus* (Bl. & Schn.) at Mandapam, S. E. India. It differs from the known species of the genus in the presence of two vaginae opening by separate pores surrounded by well developed suckers (cf. Ramalingam, 1961 b. Fig. 1-7).

Apart from the highly developed abaxial/adaxial asymmetry found in *Gotocotyla* clamps, comparable in degree only with that of *Anchorophorus* Bychowsky & Nagibina (1958) there are three other points of general biological interest which may be mentioned briefly. There is an unusual degree of polymorphism shown in the clamps of individual worms, at least in some species : this has been analysed in detail by Ramalingam (1961). A detailed exposition of the limits of variation will have to be studied before a critical assessment of this kind of species character can be made.

Hargis' (1956: 37) discovery of the characteristic single pair of anchors on the terminal lappet in *G. acanthophallus* from three different hosts (perhaps subspecies) completes the characters for the generic identity of *Lithidiocotyle* Sproston, 1946, and *Gotocotyla* Ishii, 1936. But at the same time he made the far-reaching discovery of additional larval anchors and hooklets in the anterior region of the haptor, between the clamp-rows and on the dorsal side. Unfortunately he supplies no diagram to indicate the approximate location or the number of these larval anchors, but the bare fact of their occurrence in *Gotocotyla* is highly significant. They at once recall the "body hooks" of *Pricea,* and therefore an indication of a primary dichotomy of the longitudinal growth-axes in the protohaptor — in fact, between the ultimate and penultimate pairs of hooks (posterior and posterior-laterals in the nomenclature of Llewellyn (1957 *a*), as in *Pricea.* Whereas in *Pricea* the 'metahaptor' arising from the anterior side of the formative zone produces a complete haptoral lobe independently of the body/haptor axis, none such is formed in *Gotocotyla* spp. Yet if the anchor-pairs are separated, the replication of clamps between them can be accounted for only by an early fore and aft dichotomy in the formative zone, producing new clamps which successively push the anchor-pairs farther as under. In *Gotocotyla* therefore, the formative zone must be sought perhaps in the proximal half of the haptor. The absence of an independent anteriorly growing lobe could be explained by the body/haptor axis to some extent "keeping pace", in its growth with the growth of the lateral replication axes. The occurrence of double or triple lateral rows of clamps reported for most species in the anterior region of the haptor, would indicate that the growth in the metahaptor clamp-rows had overtaken that of the median axis and a further (lateral) dichotomy took place, accommodating additional clamps medially at every second (and third) division of the 'clamp-primordium' The inability to form a ventro-anterior external metahaptor-bud would be accounted for by the original dichotomy not being sufficiently deep to involve tissues of the medium axis of the haptor—as in the delicate frilly haptor of *Microcotyle priacanthi* Meserve.

The unique features of the growth gradients in Monogenoidea would appear to separate them clearly from all other Platyhelminthes, and to indicate a very long phylongenetic history, with an exceptionally high level of organization in present-day forms on the more highly evolved fish groups: co-existing with admittedly more primitive forms on some primitive fish-groups, and in Amphibia and Reptilia.

V—SUMMARY OF THE SYSTEMATIC REVISION OF THE VALID SPECIES OF THE AXINIDAE, HETEROMICROCOTYLIDAE AND GASTROCOTYLIDAE, WITH THEIR HOSTS AND LOCALITIES

MICROCOTYLOIDEA (Unnithan, 1957) *s. str. emend.*

AXINIDAE Unnithan, 1957 (3 subfamilies)

AXININAE Monticelli, 1903 *s. str.* Unnithan, 1957. (7 genera)

Axine belones Abildgaard, 1794 : on *Belone belone* (L.) Europe.

Axine cypseluri (Meserve, 1938) Price, 1945: on *Cypselurus agoo,* Japan and *C. callopterus,* Galapagos.

Axine yamaguti (Meserve, 1938) Price, 1945, on Exocoetid sp. Mexican Pacific.

Axine parawa Unnithan, 1957, on *Cypselurus bahiensis,* S. W. India.

Axine hemirhamphae Unnithan, 1957 : On *Hemirhamphus xanthopterus,* Val. Trivandrum, SW. India.

Axine tripathii (Tripathi, 1959) Yamaguti 1963 n.n.pro *A. hemirhamphae* Tripathi 1959 (*non* Unnithan, 1957), on *Hemirhamphus georgii* Val. Hooghly R. & Orissa, NW. Bay of Bengal.

Axine inada Ishii & Sawada, 1938, on *Seriola aureovittata* T. & S., Japan.

Axinoides tylosuri Yamaguti, 1938, on *Tylosurus schismatorhynchus,* Japan.

Axinoides gracilis (Linton, 1940) Sproston, 1946, on *Tylosurus marinus* (Walb.), USA, Atlantic Coasts.

Axinoides raphidoma Hargis, 1956, on *Tylosurus raphidoma,* USA, Atlantic.

Axinoides kola Unnithan, 1957, on *Athlennes hians* (Val.), SW. India.

Axinoides sebastisci Yamaguti, 1958, on *Sebastiscus marmoratus,* Japan.

Axinoides resplendens Caballero, Bravo & Grocott, 1954, on *Tylosurus fodiater,* Columbia, E. Pacific.

Chlamydaxine truncata (Hargis, 1956) Unnithan, 1957, on *Tylosurus raphidoma,* USA Atl.

Loxura ananaphallus Unnithan, 1957, on *Tylosurus leiurus* (Blkr.), SW. India.

Loxuroides sasikala (Unnithan, 1957) Price 1962, on *Cypselurus oligolepis* (Blkr.), S. India.

Oligapta oligapta Unnithan, 1957, on *Hemirhamphus georgii,* S. India.

Indocotyle hemirhamphae Tripathi, 1959, on *Hemirhamphus georgii,* Hooghly R., & Orissa, Bay of Bengal.

HETERAXININAE Unnithan, 1957 emend. (6 genera)

Heteraxine heterocerca (Goto, 1894) Yamaguti, 1938, on *Seriola aureovittata* T. & S., Jap.

Heteraxine seriolae (Ishii, 1936) Yamaguti, 1938, on *Seriola aureovittata,* Japan.

Uraxine chura Unnithan, 1957, on *Euthynnus alleteratus affinis* (Cantor), from Kerala, India.

Uraxine macrova (Unnithan, 1957) *status nov.*, on *E. alleteratus affinis*, from Kerala, India.

Allopseudaxine katsuwonis (Ishii, 1936) Yamaguti, 1943, on *Katsuwonus vagans* (Lesson), Japan.

HETEROMICROCOTYLIDAE (Yamaguti, 1963) *s. str.* emend. (3 subfamilies)

HETEROMICROCOTYLINAE subfam. nov. (5 genera)

Heteromicrocotyla carangis Yamaguti, 1953, on *Caranx* sp. from Macassar., Celebes.

Heteromicrocotyla vaginispina Unnithan, 1961, on *Carangoides malabaricus* (Bloch & Schneider) at Trivandrum and Neendakara (South Arabian Sea).

Heteromicrocotyla polyorchis Unnithan, 1961., on *Carangoides malabaricus* at Trivandrum (South Arabian Sea).

Heterapta chorinemi Tripathi, 1956,—as *"Diplasiocotyle"* comb. nov., on *Chorinemus tala* Cuv., from Mahanadi Estuary, Bay of Bengal.

Heterapta heterapta Unnithan, 1961 (genotype), on *Chorinemus sanctipetri* Cuv., at Trivandrum (South Arabian Sea).

Dicotyle stromatea (Tripathi, 1956) comb. nov., on *Pampus argenteus* (Euphr.), from Puri, Bay of Bengal.

Dicotyle vellavoli Unnithan, 1961, on *Chandroloites* (*Stromateus*) *chinensis* (Euphr.) at Trivandrum and Vizhingom (South Arabian Sea).

Dictydenteron reticulatum (Goto, 1894) gen. n., *Pampus argenteus* (Euphr.), from Japanese Seas.

Carangiamata sagae (Manter & Prince, 1953) gen. nov., on *Caranx* sp., from Suva, Fiji.

CEMOCOTYLINAE Subfam. nov. (4 genera)

Cemocotyle carangis (MacCallum, 1913) Sproston, 1946, on *Caranx crysos* (Mitch.), USA, Atlantic.

Xureliphilus elongatus (Meserve, 1938) gen. nov., on *Xurel malampygus* Cuv., from Secas Isl., Galapagos.

Tripathiana minuta (Tripathi, 1959) gen. nov., on *Megalaspis cordyla* from Puri, Orissa, Bay of Bengal.

Megamicrocotyle chirocentrus Tripathi, 1956, and Unnithan, 1961 on *Chirocentrus dorab* (Forsk.), From Puri, Bay of Bengal and Trivandrum, Arabian Sea.

Megamicrocotyle microcotyla (Manter & Prince, 1953) Unnithan, 1961, on a 'ribbon-fish' from Fiji.

PYRAGRAPHORINAE Subfam. nov. (2 genera)

Pyragraphorus pyragraphorus (MacCallum & MacCallum, 1913) Sproston, 1946, on *Trachinotus carolinus* from USA. Atlantic.

Heteraxine carangis (MacCallum, 1918) Yamaguti, 1938, on *Caranx hippos,* from USA Atlantic Coast.

Heteraxine scomberomori Koratha, 1955 (?), on *Scomberomorus* sp., from USA Atlantic.

Heteraxine karavoli Unnithan, 1957, on *Formio niger* (Bloch), from SW. India.

Heteraxine meintoshi (Price, 1962) Yamaguti, 1963 syn. *Allencocotyla mcintoshi* Price (1962), on *Seriola lalandii* from Florida, USA.

Heteraxinoides triangularis (Goto, 1894) Yamaguti, 1938, on *Anthias schlegelii* Gunth., from Japan.

Heteraxinoides chinensis (Yamaguti, 1937) Yamaguti, 1938, on *Hapalogenys nitens* Rich. Japan.

Heteraxininoides oligoplitis (Meserve, 1938) Hargis, 1956, on *Oligoplites saurus* (Bl. & Sch.) from E. Pacific.

Heteraxinoides xanthophilus Hargis, 1956, on *Leiostomus xanthurus* Lacep., from USA Atlantic Coast.

Heteraxinoides xanthophiloides Price, 1962 on *Leiostomus xanthurus* Lecep., from USA.

Kannaphallus virilis Unnithan, 1957, on *Caranx atropus,* — SW. India.

Zeuxapta zyxivaginata Unnithan, 1957 (pro *Microcotyle seriolae* Yamaguti, non *H. seriolae Ishii*) on *Seriola aureovittata,* from Japan.

Zeuxapta meservei (Sproston, 1946) comb. nov. (pro *H. seriolae* Meserve, 1938, *non* of Ishii 1936), on *Seriola dorsalis* (Gill), from Galapagos Islands.

Gonoplasius carangis Sandars, 1947, on *Caranx georgianus,* from W. Australia.

Gonoplasius longirostri (Robson, 1961) Price, 1962, Syn. *Microcotyle longirostri* on *Longirostrum platessa* from New Zealand.

Axinoa aberrans (Goto, 1894) gen. n. (Genotype), on *Tylosurus schismatorhynchus* (Blkr.), from Japan.

Axinoa meservei (Price, 1945 — pro *Axine aberrans* of Meserve, *non* of Goto, 1894) comb. n., on *Tylosurus fodiator* from Columbia, E. Pacific.

MONAXININAE Unnithan, 1957 (5 genera).

Monaxine formionis Unnithan, 1957, on *Formio niger* (Bloch), — S. India.

Monaxine bivaginalis Ramalingam, 1961, on *Formio niger* (Bloch),— S. E. India.

Neoaxine constricta (Yamaguti, 1938) Price, 1945 : (Syn. *Amonaxine constricta* of Unnithan, 1957), on *Tylosurus schismatorhynchus,* from Japan.

Crotalaxine serpentina Unnithan, 1957, on *Athlennes hians* (Val.) from S. India.

Hargisiella hippos (Hargis, 1956) gen. n. (type species), on *Caranx hippos,* Florida, USA, Atlantic.

Hargisiella incomparabills (MacCallum, 1917) comb. nov., on *Caranx ruber* (Bloch), from USA Atlantic.

GASTROCOTYLOIDEA Price, 1959 (3 families)

GASTROCOTYLIDAE Price, 1943 (5 subfamilies)

GASTROCOTYLINAE Sproston, 1946 (5 genera).

Gastrocotyle trachuri v. Ben & Hesse, 1863, on *Trachurus trachurus,* from European and Japanese waters.

Gastrocotyle japonica Ishii & Sawada, 1938 on *Pneumatophorus japanicus* (Houttyn), from Japan.

Gastrocotyle indica Subhapradha, 1951, on *Caranx kalla* Cuv., from Madras, Bay of Bengal.

Gastrocotyle kurra Unnithan, 1968, on *Caranx kurra* Cuv., from Trivandrum, Arabian Sea.

Gastrocotyle kalla Unnithan, 1968, from *Caranx kalla* Cuv., from Trivandrum, Arabian Sea.

Chauhanea madrasensis Ramalingam, 1953, on *Sphyraena acutipinnis* and *S. commersonii* Cuv., resp. from Madras and Madagascar.

Yamaguticotyla truncata (Goto, 1894) Price 1959, on *Parapristipoma trilineatum* from Japan.

Churavera macrova Unnithan, 1968, on *Euthynnus affinis* (Cantor) from Trivandrum, Arabian Sea.

Eyelevera typica Unnithan, 1968, on *Rastrilliger karagurta* (Cuv.) at Trivandrum, Arabian Sea.

THORACOCOTYLINAE Subfam. nov. (4 genera).

Thoracocotyle crocea MacCallum, 1913: on *Scomberomorus maculatus* (Mitchill), USA, Atlantic, & Mexican Pacific.

Thoracocotyle ovalis Tripathi, 1956 (emend. orthogr. 1959): on *Scomberomorus guttatus* NW. Bay of Bengal.

Dawesia indica Unnithan, 1964, on *Scomberomorus guttatus* (Bl. & Schm.) at Trivandrum, Arabian Sea.

Lintaxine cokeri (Linton, 1940) Sproston 1946: on *Aplodinotus Grunniens* Raf., Iowa, USA.

Amphipolycotyle chloroscombris Hargis, 1957: on *Chloroscombrus chrysurus* (L.), S. USA, Atlantic.

PRICEINAE Chauhan, 1953, *s. str. emend.* (4 genera)

Pricea multae Chauhan, 1945, (genotype): on *Cybium lineolatum* Cuv., Bombay, E. Arab. Sea.

Pricea minimae Chauhan, 1945: on *Katsuwonus pelamys,* Bombay.

Pricea microcotylae Chauhan, 1945: on *Rastrelliger kanagurta,* Bombay.

Pricea tetracantha Ramalingam, 1952, on *Scomberomorus guttatus* (Bl. & Sch.), Madras, W. Bay of Bengal.

Pricea armata Ramalingam, 1952, on *Scomberomorus guttatus* (Bl. & Sch.), Madras, W. Bay of Bengal.

Pricea tricantha Ramalingam, 1952, on *Scomberomorus guttatus* (Bl. & Sch.), Madras, W. Bay of Bengal.

Pricea melane Ramalingam, 1952, on *Scomberomorus guttatus* (Bl. & Sch.), Madras, W. Bay of Bengal.

Pricea minuta Ramalingam, 1952, on *Scomberomorus guttatus* (Bl. & Sch.), Madras, W. Bay of Bengal.

Pricea robusta Ramalingam, 1952, on *Scomberomorus guttatus* (Bl. & Sch.), Madras, W. Bay of Mengal.

Neothoracocotyle coryphaenae (Yamaguti, 1938) Hargis, 1956 (Genotype), on *Coryphanena hippurus* L., Japan.

Neothoracacatyle acanthocybii (Meserve, 1938) Hargis. 1956, on *Acanthocybium solandri* (C.) Galapagos.

Scomberocotyle scomberomori (Koratha, 1955) Hargis, 1956, on *Scomberomorus maculatus*, & *S. cavalla*, S. USA, Atlantic.

Pseudaxine trachuri Par. & Per., 1890 (genotype), on *Trachurus trachurus* (L.), Europe and Japan.

Pseudaxine vagans Ishii, 1935, on *Katsuwonus vagans* (Less.), Japan.

Pseudaxine mexicana Meserve, 1938, on *Scomberomorus maculatus* (Mitchill), *S. cavalla* (Cuv.), Mexican Pacific and S. USA, Atlantic.

Pseudaxine indicana Chauhan, 1945, on *Sparus berda* Forsk., Bombay.

Pseudaxine kurra Unnithan, 1968, on *Caranx kurra* Cuv. & Val. at Trivandrum, Arabian Sea.

ENGRAULICOLINAE Subfam. nov.

Engraulicola forcepopenis George, 1960, from *Anchoviella betaviensis* (Hardenberg) at Trivandrum, Arabian Sea.

Engraulicola micropharyngella Unnithan, 1967, from *Anchoviella commerssoni* (Lacepi) at Trivandrum, Arabian Sea.

Engraulixenus malabaricus Unnithan, 1967, on *Thrissocles malabaricus* (Bloch) at Trivandrum, Arabian Sea.

Engrauliphila grex Unnithan, 1967, on *Thrissocles dussumieri* (Val.) at Trivandrum, and Ayrumthengu, Arabian Sea.

Engrauliscobina thrissocles (Tripathi, 1959) gen. nov., on *Thrissocles mystax* at Puri, N.W. Bay of Bengal.

Engrauliscobina triaptella Unnithan, 1967, on *Thrissocles dussumieri* (Val.) at Vizhingom, Trivandrum, Arabian Sea.

Pellonicola elongata Unnithan, 1967, on *Pellona* (Illisha) *brachysoma* (Blkr.) at Trivandrum, Arabian Sea.

GOTOCOTYLINAE Subfamily nov. (one genus)

Gotocotyla sawara Ishii, 1936 (genotype): on *Cybium niphonium* Cuv., Japan.

Gotocotyla Ishii, 1936 (Syn. *Lithidiocotyle* Sproston, 1946; *Microcotyle auct.*; *Pseudomicrocotyle* Sandars 1947).

Gotocotyla acanthura (Par. & Per., 1896) Meserve, 1938, on *Brama rayii* (L.), European Seas.

Gotocotyla lintoni nom. nov. pro *Microcotyle* sp. of Linton, 1906, on *Pomatomus saltatrix*, USA, Atlantic.

Gotocotyla acanthophallus (MacCallum & MacCallum, 1913) comb. n., on *Roccus saxatills* USA, Atlantic.

also (?) sub spp. on *Scomberomorus maculatus* & *S. cavalla*, USA, Atlantic.

Gotocotyla elagatis Meserve, 1938, (Syn. *Pseudomicrocotyle elagatis* Sandars, 1947 (?), on *Elagatis bipinnularis* (Quoy & Gaim), off Ecuador, E. Pacific, & S. Australia.

Gotocotyla meservei Yamaguti, 1953, on *Elagatis* sp., Celebes.

Gotocotyla secunda (Tripathi, 1956) comb. n., on *Scomberomorus guttatus* (Bl. & Schn.), NW, Bay of Bengal.

Gotocotyla bivaginalis (Ramalingam, 1961) comb. n., on *Scomberomorus guttattus* (Bl. & Schn.), SE India.

(Total reviewed: 107 spp.).

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VII — SUMMARY

An analysis of the dynamics of axial growth potentials in the haptoral region of the higher Monogeneoidea reveals, 1) the presence of a characteristic growth gradient arising in the protohaptor (the anchor-bearing ventral lobe of the larval haptor), and controlling the successively anterior replacements of the lateral hooklets of the larva by the 4 pairs of primary clamps. 2) Secondary growth stimuli may induce a potentially unlimited forward replication of the primary clamps (in Microcotyloidea and Gastrocotylidae). 3) inhibitory influences may be secondarily imposed, usually differentially, on the two lateral replication-axes. 4) Various degrees and kinds of asymmetry may be the result of interactions of differential inhibitions and postural stresses. 5) The effects of secondarily imposed growth-stimuli, particularly characteristic of Heteromicrocotylidae Yamaguti, 1963, *s. str. emend.* as inhibitory influences are of Axinidae Unnithan, 1957, in the clamps themselves are usually abrupt; remodelling and increase in size often affects only the last-formed primary clamps, and may be unilateral or bilateral (e.g. *Paramazocraes* Tripathi, 1959, *Pseudoanthocotyle* Bychowsky & Nagibina, 1954, *Anthocotyle* v. Ben. & Hesse, and *Xureliphilus elongatus* (Meserve) comb. n., and in forms with secondary growth stimulation it is persistent at the same intensity. 6) Replication

stimuli, on the other hand, may appear later in life, and in the secondary part of the euhaptor, when a lateral dichotomy occurs in the replication axes resulting in more than a single file of clamps on each side. 7) more frequently, replication stimuli are imposed at various levels in the larval haptor, when there is a transverse scission in the formative zone on one or both sides, producing an anterior-posterior dichotomy of the replication axis of one or both sides, forming respectively a unilateral or bilateral metahaptor.

A systematic revision in the light of these findings, and of a reconsideration of the comparative morphology of the clamps, has led to give preference to the latter criteria for the higher taxa, since secondary growth of various degrees in the haptor may have been developed in more than one evolutionary line its characters not being exclusive to those of clamp-type. The outcome is the re-introduction of superfamilies and the elevation of 6 of Bychowsky's 7 families of the suborder Discocotylinea to superfamily rank. Microcotyloidea (Unnithan 1957) *s. str. emend.* has 3 families: Microcotylidae *s. str.*, Axinidae Unnithan, 1957, and Heteromicrocotylidae Yam. 1963 *s. str. emend.*; Gastrocotyloidea Price 1959, has 4 families: Anthocotylidae Bych. 1957, Opisthogynidae Unnithan 1962, Gostrocotylidae Price 1943 and Gephyrocotylidae Unnithan, 1966. Present detailed revision covers only the families Axinidae, Heteromicrocotylidae, and Gastrocotylidae: some emendations have been made in the definitions of the first, and some new allocations, including the new genus *Axinoa.* Four new subfamilies have been created for the second, and 4 genera are new; the last contains the subfamilies Gastrocotylinae Sproston, 1946, Thoracocotylinae nov., Priceinae *s. str. emend.*, Engraulicolinae nov., and Gotocotylinae nov. considerable rearrangement is suggested and 2 new genera: the total *novae,* 6 subfamilies, 9 genera, 3 spp. n., some 18 new combinations and several orthographical emendations for species and hosts are tabulated among the list of over 107 species reviewed, with their hosts and localities.

Comparative morphology of the clamps suggests that there has been a re-evolution of the sucker type of adhesive unit, but this return to the mode of the Polyopisthocotylinea is structurally a far more complex one in the higher Discocotylinea (even more complex in Hexostomatidae, but two simpler types in Mazocraeidae). Essentially it is an opened clamp in which asymmetrical stresses have distorted the sclerites and brought about a redevelopment of the adductor muscles to form a *framed* acetabulum. The different types of "open-clamp-sucker" are characterized by their mode of distortion and the decreasing number of sclerites contribute to their framework. This has probably evolved independently 6 times in Discocotylinea: a deep muscular cup supported by thick cylindrical simplified jaws and the meridional spring in *Uraxine;* the jaws opening like the hinged lid of a box, the C-shaped rami of both jaws forming the quadrants of the open sucker in species belonging to the Heteromicrocotylinae; but in *Heteromicrocotyle* itself, the sessile clamps have opened rather like a fan, and the spring has a roof-support developed from its expanded end, the ventral jaws forming more than half the frame; while in the series *Lintaxine, Amphipolycotyle, Thoracocotyle, Dawesia* the clamp has opened like a book, the ventral jaw-rami alone contributing to the frame, the dorsal jaw-rami being jettisoned outside the rim along with the oblique sclerites; the rib-like thickenings in the capsule wall are only developed in *Thoracocotyle* in this series, but they are incidental to the clamp mechanism in practically all the many genera in which they occur, hence their elimination as a diagnostic criterion of the subfamily Priceinae as originally conceived. The "open-clamp-sucker" in *Diclidophoropsis*. appears to be a simple box-lid opening with asymmetrical quadrants framed by the rami of both jaws, but in *Choricotyle* spp. and some *Diclidophora* sensu lato, the highly asymmetrical diclidophorid clamp has become secondarily distorted (see Bychowsky 1957, figs. 303-306) and the abaxial-anterior sucker is framed by the median spring and the abaxial ramus of the ventral jaw.

Secondary growth phenomena in the haptor, combined with the various other peculiarities are considered valid criteria for separating Monogeneoidea from all the rest of Platyhelminthes, and indicative of their very remote ancestry.

VIII — REFERENCES

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