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Studies on the genus *Lancetes*. 2. Analysis of its phylogenetic position using preimaginal characters (Coleoptera, Dytiscidae)

by S. Ruhnau & M. Brancucci *

Abstract: Several, mostly primitive larval and pupal characters of the genus *Lancetes* contradict its usual placement «in the middle» of the Colymbetinae. The larvae of a few other genera likewise contribute to a certain heterogeneity in this subfamily. The present analysis of many larval and pupal characters of dytiscids is focused on working out the «monophyletic core» of the subfamily Colymbetinae, and on searching for the actual sister-group of the genus *Lancetes*. The results are: *Lancetes* belongs to the undoubtedly monophyletic group ‘all Dytiscidae without Copelatini’; *Copelatus* and its allies are removed from the Colymbetinae and form the sister-group of the remaining Dytiscidae. ‘*Lancetes* + Colymbetinae (excl. *Agabetes*) + Dytiscinae’ are surely a monophyletic group, and each of the three subgroups themselves can be established as monophyletic. So far, a definitive statement on the sister-group relationships amongst these three groups cannot be given.

I. Introduction

During our study on *Lancetes angusticollis* Curtis (BRANCUCCI & RUHNAU, in press), some doubts have appeared whether the transantarctic dytiscid genus *Lancetes* actually belongs to the subfamily Colymbetinae. Some pupal and larval characters of *Lancetes* seem to argue against this usual subfamilial placement. BEIER (1928) already called attention to this problem.

The present study, based on detailed comparisons of a large number of larval and pupal characters should contribute towards a solution to the questions: Are the Colymbetinae monophyletic, including or excluding *Lancetes*? What is the sister-group of *Lancetes*?

The analysis is arranged in 7 consecutive steps; plesiomorphic character states are indicated by a, b, c, etc., (syn)apomorphies by a', b', c', etc. According to the principles of Hennig-type analysis (HENNIG, 1981), only the close agreement in (probable) synapomorphies give evidence for the monophyly of the respective group. *Lancetes* will be treated as

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separated from any subfamily, as long as its position is not clarified. We designate 1st, 2nd, and 3rd larval instars as L₁, L₂, and L₃, respectively. The term primary (e.g. primary setae) is used to indicate only characters of L₁; primary characters may be evident, indistinct, or absent in L₂₋₃. Pupal setal terminology follows BERTRAND (1928) and BRANCUCCI & RUHNAU (in press). Many of the characters used are illustrated in the cited studies.

Most taxa that we directly examined were Palearctic; character states of non-Palearctic taxa were obtained from the literature cited. While writing the final draft of this paper, we received material of two interesting Nearctic colymbetine genera deviating in some characters from those of European members of the subfamily (L₃ and pupa of *Matus*, and L₃ of *Coptotomus*), and also of the Nearctic genus *Agabates* (L₂₋₃); their characters caused some unexpected changes in our argumentations.

As will be seen below, our results confirm two important conclusions of BURMEISTER (1976) who, using the female ovipositor, clearly showed that two genera, hitherto placed in the Colymbetinae, have to be removed from them: *Agabates*, which he linked to Laccophilinae, and *Copelatus*, whose precise relationships to other dytiscids remained unresolved by him (he did not examine the genera *Lancetes* and *Matus*).

II. Phylogenetic analysis

Step 1: Synapomorphies of 'Dytiscidae (incl. *Lancetes*) excl. Copelatini'

The tribe Copelatini probably comprises 4 genera (see below) with nearly 500 species; however, preimaginal stages are only known of some species of *Copelatus* (BERTRAND, 1972). These differ from those of other dytiscid groups in many, mostly plesiomorphic characters.

Plesiomorphies of *Copelatus* (as a member of the Copelatini)

Synapomorphies of all other Dytiscidae

Larvae

a. Prepharynx relatively long, totally open in front, and without	a'. Prepharynx somewhat shortened, modified into a trans-
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a constriction at its end, leading broadly into the very wide pharynx.

(see DE MARZO (1979) for details of characters a-c, a'-c')

- b. Presence of a drawn-out wide crop and of a well-developed proventriculus. Origin of midgut at end of thorax.
- c. Tentorial bridge strongly arched forward (similar to, but not so extremely arched as in *Hygrobia* and *Amphizoa*), branching off far rearward from the «caudal arms» of tentorium (RUHNAU, in press).
- d. Prey is squeezed by the weakly and broadly sulcate, non-channeled mandibles into the prepharynx; there, sometimes, only the body fluid of the slightly damaged prey is sucked out; often, however, the prey is swallowed whole (also confirmed by WATTS, 1963).

verse sucking chamber; in front, the large middle part of the «mouth» is closed (or at least functionally well closible) by the approach of epipharyngeal and hypopharyngeal areas (= development of the «coaptation»); only the «mouth angles» remain open; end of prepharynx very constricted. Pharynx strongly narrowed.

- b'. Crop and proventriculus totally reduced. Origin of midgut at end of head capsule (sometimes even already behind in the head).
- c'. Tentorial bridge rectilinear and short, branching off anteriorly from the «caudal arms» (KORSCHELT, 1923:610) (bridge secondarily lost in [all?] Hydroporinae).
- d'. Digestive fluid is injected through the deeply grooved to well-channeled mandibles into the prey; by the same way, the predigested, liquefied contents of the prey are sucked into the prepharynx. (The deep mandibular grooves have not become closed immediately to perfect channels in all the subgroups of this group, e. g. in *Agabetes* (DE MARZO, 1976c) and in *Lanctetes* (see below, character 5 b).

e. Pegs of the labral¹ edge not flattened, very small, somewhat cone-shaped (similar to *Hygrobia*).

e'. Pegs of labral edge dorso-ventrally flattened (lamelliform) (at least from L₂), and mostly very prolonged and broadened. Movement of these labral lamellae restricted to ventro-oral direction by means of a dorso-anterior stop mechanism.

f. Ventral side of abdominal segment VIII well-sclerotized backward only half-way up to the anal-cercal region; only this part seems to correspond to sternite VIII (cf. the unusual position of the posterior setae of sternite VIII in *Copelatus*, discussed below under character 7 a'). The subsequent area up to the membranous anal region is occupied by a rectangular, glabrous, semimembranous, slightly convex «plate», narrowly surrounded by membranous cuticula (DE MARZO, 1976a: Figs 4 and 8); probably the «plate» represents the ancestral sternite IX.

f'. Ventral side of abdominal segment VIII well-sclerotized backward as far as the anal-cercal region (prolonged sternite VIII). A novel peculiar «tendon plate» lying horizontally in the plane between posterior rectum and prolonged sternite VIII seems to correspond to the sternite IX seen in *Copelatus*, but modified and displaced internally. The attachments and courses of certain muscles suggest our interpretation: The ventral longitudinal muscles, originating far antero-laterally from sternite VIII, converge backward inserting at anterior edge of the «tendon plate»; caudally from the «tendon plate» some very fine muscle strands originate backward, some leading ventro-medially toward the anus, and others diverging to the direct proximity of the cercal bases; further, some short ventral rectal muscles originate dorsally

¹ The labral pegs are usually called clypeal lamellae or pegs, following the interpretation of the fore-edge of head in dytiscids as clypeal given in KORSCHELT (1923, 1924). For the reasons why we interpret them as labral, ref. RUHNAU (in press).

g. Bases of cerci cylindrical, and widely separated from each other and from the undistinctly defined lateral edge of the prolonged tergite VIII by membranous areas.

from the «tendon plate» (KORSCHELT 1923:673–675).

g'. Bases of cerci enlarged, medially excavated and proximate to each other; stretched cerci laterally touching the strengthened, well-defined lateral edge of prolonged tergite VIII (this edge forms a special gliding edge for a more precise guide of stretching movements of the cerci).

Note: In 'Dytiscinae excl. Cybisterini' the conditions of cercal bases are secondarily modified in connection with the acquisition of a precise lateral articulation point of cercal bases, each with a small acute, triangular tergal process.

Pupae

h. Absence of setae on sternum VIII (suspected plesiomorphy). The only sternal setae present in *Copelatus* are 1 pair on sternum VII in *C. haemorrhoidalis* (F.) (correction to BERTRAND, 1928), and additionally 1 further pair on sternum VI in *C. glyphicus* (Say) (SPANGLER, 1962) (in *Hygrobia* and *Amphizoa* sternal setae are lacking).

h'. Presence of 1 pair of setae on sternum VIII in the ground-plan. Often further sternal setae present, at least 1 pair on sternum VII; only in the Hydroporinae, probably except of *Laccornis* (SPANGLER & GORDON, 1973), sternal setae are secondarily lost (correction to BERTRAND, 1928).

Note: For the distinction between sternal and pleural setae (ref. BERTRAND, 1928, 1972, and BRANCUCCI & RUHNAU, in press).

Conclusion

The close agreement in undoubtedly apomorphic larval characters between all dytiscids including *Lancetes* but excepting the Copelatini proves these characters to be true synapomorphies inherited from a single stem-species in the past. So the Copelatini must be excluded from this monophyletic main group of the Dytiscidae, not only from the Colymbetinae, as done by BURMEISTER (1976). On the other hand, the monophyly of the whole family Dytiscidae (including Copelatini) is beyond dispute and can be proved by about ten significant preimaginal synapomorphies (RUHNAU, in press).

Unfortunately, the monophyly of the Copelatini (i. e. *Copelatus*, *Aglymbus*, *Lacconectus*, *Agaporomorphus*) has not yet been clearly established. *Stictogabus* hitherto suspected to belong to the Copelatini, really belongs to *Platambus*, based on adult structures (BRANCUCCI, unpubl. results). Provided that the Copelatini are monophyletic, our results conclusively show that the Copelatini and the group 'Dytiscidae excl. Copelatini' are sister-groups.

Note: The Noteridae, hitherto mostly considered as nearest to the Dytiscidae, cannot be placed within the clearly monophyletic group 'Amphizoidae + Hygrotiidae + Dytiscidae' (RUHNAU, in press); in order to recognize plesiomorphic or apomorphic states of preimaginal dytiscid characters we primarily regarded the conditions found in *Hygrotus* and *Amphizoa*.

Step 2. Synapomorphies of 'Lancetes + Colymbetinae + Dytiscinae'

Larvae

a'. Intercercal sclerite developed (L_{1-3})

Dorsocaudally from the anus, between the bases of the cerci, a distinct sclerite has been developed (the so-called «tergite IX» after KORSCHELT, 1924: 446,560; see also FIORI, 1948; DE MARZO, 1973). This sclerite is triangular in shape with its acute angle directed dorsally (ground-plan of the group). At the 2 rather obtuse ventrolateral angles of this somewhat convex sclerite, a paired, thin muscle arises inserting at the lateral base of each cercus (in a big part of the Dytiscinae, the shape of the intercercal sclerite is modified and functionally improved possessing two muscle pairs inserting at the cercal bases; RUHNAU,

unpubl. results). This arrangement, lacking in the other dytiscids, enables a more precise mobility of the cerci, which seems to be useful for the respiration posture of the larvae. In the plesiomorphic condition, seen in all other Dytiscidae (except of *Agabetes*), the intercercal region is completely membranous (L_{1-3}); possibly comparable muscles possess another course. In *Agabetes*, we observed a somewhat similar intercercal sclerotization, but of another, more transverse shape (SPANGLER & GORDON, 1973). We presume that this feature arose convergently, as BURMEISTER's (1976) linkage of the genus to the Laccophilinae appears convincing; this linkage is also supported by the presence of a nearly identical jumping device in *Laccophilus* and *Agabetes* (RUHNAU, unpubl. results).

b'. 1 pair of «presternite plates» developed on prothorax

These new sclerites, being rather small in the ground-plan of the group, become more or less enlarged in various Colymbetinae, and, especially, in all Dytiscinae; in a great part of the latter, the group 'Dytiscinae excl. Cybisterini', the plates are fused to an unpaired presternite. All other dytiscids (incl. *Agabetes*) and *Hygrobia* lack any distinct sclerification in the presternal area in front of the episterna.

With the acquisition of presternite plates, the following 2 muscles – present in all Dytiscidae – obtain a solid base for their attachments. In those genera with primitively small presternite plates (e. g. *Lancetes*, *Agabus*, *Platambus*), the ventral attachment points of these muscles are clearly more concentrated compared with the conditions in those dytiscids lacking such plates (numbering of muscles according to KORSCHELT, 1923: 637–641).

M I₆: From the presternite plate to the (dorso)lateral edge of the head capsule foramen (levator capitis verticalis).

M I₉: From the anterior half of pronotum, sublaterally, to the presternite plate (inner dorsoventral muscles). In all dytiscids except of Dytiscinae, M I₉ consists of two thin bundles: in the Dytiscinae the bundles get more or less modified, and often multiplied.

c'. Joint 1 of labial palps longer than joint 2 (distinct at least in L_3)

Secondary bipartitions of the 2 palpal joints, occurring in some Dytiscinae, do not change the stated proportions between the recognizable primary sections. In L_1 the lengths of the palpal joints partly reflect more primitive conditions than in L_3 : thus *Lancetes*- L_1 shows its joint 1

still shorter than joint 2, whereas in L_1 of Colymbetinae and Dytiscinae joint 1 is at least of equal length. In L_3 of other dytiscids joint 1 is primitively clearly shorter than joint 2 (*Copelatus*, *Agabetes*), like in *Hygrobia* and *Amphizoa*; in *Laccophilus* the joints are of equal length, and in some Hydroporinae joint 1 is slightly longer than joint 2 (suspected parallel developments).

d'. Loss of the «outer anterior dorsoventral muscles» of prothorax

In the anterior half of the prothorax, adephagan larvae usually possess 2 series of dorsoventral muscles: a sublateral one (= the above mentioned $M I_9$), and another series, well-separated from the first in a completely lateral position (= «outer anterior dorsoventral muscles»). Possibly these outer muscles should be better named «outer tergopleural muscles», interpreting their insertions on the membrane just below the pronotal edge as pleural. These outer muscles are absent in the group of dytiscids under consideration (supposed synapomorphy). All other dytiscids (except *Agabetes*?) possess at least 2 fine flat bundles of these muscles. In *Agabetes* we did not find these outer muscles as expected, but possibly because the musculature of the larvae at hand was not preserved well enough.

e'. L_1 -mandibles with 5 primary sensilla placoidea (instead of 4)

In dytiscids, and for the first time in *Hygrobia*, the L_1 -mandibles possess a set of 4 primary sensilla placoidea, named P_1 , P_2 , P_3 , P_5 by DE MARZO (1976c, 1977, 1978). A further primary sensillum, named P_4 , placed dorsally, subdistally on the mandible, is only present in the considered group. In Colymbetinae and Dytiscinae P_4 is distinct in L_1 (except of *Hydaticus* and *Cybister*, where its recognition provides difficulties (DE MARZO, 1977)), but normally undistinct in L_{2-3} ; in *Lancetes*, however, it remains large and distinct up to L_3 .

DE MARZO (1978) suggested that P_4 should be homologized to the exterior mandibular seta, situated about at midlength on L_1 -mandibles of Hydroporinae, Laccophilinae, and *Copelatus*, and named by him « T_1 ». But *Lancetes*- L_1 possesses both (!) the «new» subdistal sensillum P_4 and the «old» adephagan seta T_1 , typical for carabids (BOUSQUET & GOULET, 1984) and various Hydradephaga.

Pupae

So far, we have difficulties in perceiving joint derived features in

the pupae of the group under consideration; a synapomorphic trait could be:

f'. Area of frons between the eyes markedly flattened or even depressed (ref. BRANCUCCI & RUHNAU, in press).

One exception within the Colymbetinae (although possibly due to fixation): we observed that the single known relatively intact pupal specimen of *Matus* (WOLFE & ROUGHLEY, in press) shows its area of frons not flattened. Convergently to the considered group, the hydroporine genus *Hyphydrus* has its area of frons similarly depressed.

Conclusion

Evidence for the monophyly of the group 'Lancetes + Colymbetinae + Dytiscinae' seems to come from the outlined larval synapomorphies (Fig. 1). The question of its sister-group – probably formed by 'Laccophilinae incl. Agabetae + Hydroporinae' – is not the subject of this paper.

We observed one apomorphic peculiarity which seemingly ran counter to our conclusion, which would link *Lancetes* with *Laccophilus*. Both genera (BRINCK, 1945; DE MARZO, 1976b) show in their L_1 the same strongly reduced number of labral lamellae: 2 paramedial broad lamellae, and 2 sublateral thin «spines» with a thick socket, i. e. a special 4-peg-pattern. We consider this pattern to have arisen convergently, regarding the above listed counter-arguments². Further, according to BARMAN (1972), L_1 of *Coptotomus* shows the same unusual 4-peg-pattern; the respective conditions in L_1 of *Agabete*s and *Matus* are unknown. In the ground-plan of 'Dytiscidae + Hygrobia + Amphizoa' the basic number of labral lamellae resp. pegs is a dozen (L_1), and 4 pegs are the constant plesiomorphic number seen in carabids and gyrinids (RUHNAU, in press). Thus the reduced set of 4 pegs exceptionally present in the dytiscid genera *Laccophilus*, *Lancetes*, and *Coptotomus* seems to be an atavistic «reaparition» of the old pattern. The question of whether or not the 4-peg-pattern in L_1 of *Lancetes* and *Coptotomus* arose «only once» will be discussed below.

² A further argument against such a linkage of *Lancetes* to *Laccophilus* is a hitherto unrecorded peculiar synapomorphy shared by pupae of *Laccophilus* and *Hydroporinae*, but absent in other dytiscids: abdominal sterna V and VI posteromedially with a longer tube-like, caudally adpressed membranous outgrowth, each (RUHNAU, unpubl. results).

Note: BRINCK (1945) mentioned the 2 paramedial lamellae of *Lancetes*-L₁ as being «ciliated», which is in error.

Step 3. Synapomorphies of 'Colymbetinae excl. Lancetes'.

Larvae

a'. Frontal tubercles of L₁ (egg-bursters) markedly shifted anteriorly

The paired egg-bursters appear to have been shifted directly forward while remaining parallel, having clearly lost the immediate proximity to the frontal lines behind them; they show only a point, no longitudinal ridge, and are embedded anteriorly in a characteristic, caudally extended cuticular area which is especially extensible or elastic during hatching (JAMES, 1969; DE MARZO, 1974a, 1974b; for *Coptotomus* cf. BARMAN, 1972, Fig. 32; *Matus*-L₁ is unknown).

In the plesiomorphic condition, seen in *Lancetes* (BRINCK, 1945), in the ground-plan of Dytiscinae, and in *Copelatus*, the frontal tubercles are placed behind on the posterior margin of the frons, nearly contacting the frontal lines behind them, level with the posterior stemmata. In *Lancetes* the tubercles possess (primitively?) a short longitudinal ridge up to the anteriorly directed acute point.

b'. Accessory sensorial appendage of antennae nearly completely reduced

Hygrobia and nearly all dytiscids except for the Colymbetinae possess a joint-like, moderately to well developed appendage placed distally on antennal joint 3 beside joint 4 («antennae biramous»). Few special cases are known: it is absent in *Dytiscus*, unlike other Dytiscinae, and it is minute, but still joint-shaped in *Lancetes* (BEIER, 1928).

In «all» Colymbetinae it has disappeared as an appendage and seems to be completely included distally in joint 3 (JAMES, 1969, Figs 47, 48). Its remainder is rarely recognizable as a small, slightly convex sense organ (*Senilites*, BRINCK, 1948; *Platambus*). This generalized statement has obviously to be corrected after now that we have received material of the unusual colymbetine genera *Matus* and *Coptotomus*, as well as additional papers about them. We observed in these genera a surprisingly short antennal joint 4 (length less than $0.25 \times$ the length of joint 3, instead of the proportion of at least 0.5 found in all other Colymbetinae, and in *Lancetes*), accompanied by a clearly present

sensorial appendage as a very slender acute joint in *Coptotomus* (BARMAN, 1972), and as a very short, apically rounded one in *Matus* (WOLFE & ROUGHLEY, in press). After the evaluation of the distribution of many other characters, of which only a part is used in this paper, we interpret the presence of the sensorial appendage in *Matus* and *Coptotomus* independent of its presence in *Lancetes*. *Matus* and *Coptotomus* share a number of apomorphies with the Colymbetinae, even some with the Colymbetini s.str., whereas in *Lancetes* the corresponding features are either absent, or in a plesiomorphic state compared with those of all Colymbetinae (see also discussion below). Thus the curious presence of the antennal appendage in *Matus* and *Coptotomus* could be explained as a «reappearance» correlated with the attendant diminution of antennal joint 4. If this interpretation is correct, then the statement that the antennal appendage has disappeared in the ground-plan of Colymbetinae is nevertheless justified.

c'. Area of the origins of the dorsal cibarial dilators forming a strongly transverse band

In *Lancetes*, Colymbetinae, and Dytiscinae the muscles dlc I + II (DE MARZO, 1979) originate from a nearly rectangular common area on both sides of the midline on the clypeal region. This area is densely occupied by numerous muscle strands, at least in L_{2-3} . In L_3 of *Lancetes* and of Dytiscinae this area is roughly subquadratic and rather large, in *Lancetes*, like in *Dytiscus*, somewhat transversely extended (about 1.3 times broader than long). In (nearly) all Colymbetinae, however, this area is at least 2.5 times broader than long thus forming a transverse, often markedly light-coloured band on both sides of midline. Two exceptions within the Colymbetinae: *Coptotomus*, whose labral region has anteriorly protruding lobes, shows a less transverse muscle attachment area pointing obliquely forward medially, and *Matus* has this area relatively subquadratic (probably secondarily).

d'. Spiracles of segments I–VI (L_3) laterally joint to, or even included in the tergites

More than that, a part of the Colymbetinae show noticeably dorsally migrated spiracles (*Senilites*, BRINCK, 1948; *Matus*, SPANGLER & GORDON, 1973; *Colymbetes*, *Rhantus*, *Meladema*). The exceptional case of *Coptotomus* showing its spiracles outside of the tergites, but fully dorsally directed, may be well explainable as a secondary adaptation: its tergites are reduced in size, the pleural region bulges strongly bearing

the unique lateral tube-like gills; the weakly sclerotized, somewhat small tergites facilitate the undulatory swimming movements of the body.

In *Lancetes* the spiracles I–VI are situated laterally in the pleural membrane, and a marked distance from the tergites (probable plesiomorphy).

e'. Tendon plate in segment VIII long and narrow (L_3)

As outlined above (character 1 f'), the ventral longitudinal muscles in segment VIII converge rearward, inserting at the anterior end of a peculiar tendon plate in the monophyletic group 'Dytiscidae excl. Copelatini'. In all Colymbetinae without exception the tendon is long, rather narrow, and becoming more so in caudal direction; it begins on level with the last $\frac{1}{4}$ th of the sclerotized sternum VIII (at least in L_3). In *Lancetes* the tendon plate is small, short and subquadratic in L_{1-3} ; it is relatively well sclerotized and placed far caudally, on level with the last $\frac{1}{8}$ th of the sclerotized sternum. This situation appears to be clearly primitive. Generally the tendon plate is well recognizable through the semi-transparent sternal cuticula in larvae preserved shortly after having moulted.

In most Dytiscinae (*Cybister* seems to be atypical and needs further study), the conditions are similar to that of Colymbetinae, at least in L_3 . Possibly this feature will turn out to be a synapomorphy of these two subfamilies. But parallel development is thinkable, as shown by the probably monophyletic group 'Agabetae + Laccophilinae + Hydroporinae' possessing a very long, narrow tendon plate, but probably with slight changes in the number of the muscle strands involved.

Conclusion

The monophyly of the group 'Colymbetinae excluding *Lancetes*' can be evidenced by five synapomorphies (see also step 5). As will be shown, especially below in the discussion, single peculiar similarities of *Coptotomus* and or of *Matus* to conditions found in *Lancetes* have to be explained as secondary developments.

Step 4. Synapomorphies of the Dytiscinae (excl. *Lancetes*)

Larvae

a'. Presence of subdivisions of antennal and maxillary palpal joints

This feature is unique among Dytiscidae, and appears from L_2 in the ground-plan (in Cybisterini in L_1 as well); at least single joints are subdivided.

b'. Abdominal segments VII (from L_2) and VIII (from L_1) laterally with a dense fringe of long, stiff swimming hairs³

As a result the Dytiscinae possess a novel strong propulsion organ used in their characteristic shrimp-like escape behavior and often in their jerky prey capture behavior.

Coptotomus is the single genus outside of the Dytiscinae possessing a comparable lateral fringe on abdominal segment VIII. However, BURMEISTER (1976) has convincingly shown that this genus shares a number of derived characters in the ovipositor of adults with other Colymbetinae, especially with his Colymbetini in sensu lato, and as having the following phylogenetic position: '*Ilybius* + (*Coptotomus* + (*Colymbetes* + (*Rhantus*+*Meladema*))). Several larval and pupal characters of *Coptotomus* (see discussion below; WILSON, 1923) have to be interpreted in the same light. Therefore we consider the mentioned lateral fringe of *Coptotomus* as having arisen convergently.

c'. Femora, tibiae and tarsi dorsally and ventrally with dense fringes of long fine swimming hairs (from L_1 on)

The ventral fringe on femur, tibia and tarsus (on the latter at least developed in its proximal half) is a unique feature among Dytiscidae. A ventral femoral fringe has convergently arisen in some tropical genera of Hyphydrini and Vatellini (Hydroporinae) (BERTRAND, 1972). Dorsal fringes of swimming hairs, if present in non-dytiscine larvae (e.g. *Lanceutes*, various «higher-grade» Colymbetinae, various Hydroporinae), never appear before L_2 .

d'. Main tracheal tubes very enlarged and laterally compressed from L_1 on

The main tracheae in L_1 of all other dytiscids are exclusively nar-

³ Within the Dytiscinae, *Hydaticus* shows the fringes on segment VII in L_1 as well.

row and highly cylindrical (for tracheal conditions in dytiscid L₂, ref. below character 5 a').

Pupae

e'. Loss of the setae at wing bases and in laterotergal position on meso- and metanotum

The pterothoracal segments of Dytiscinae bear exclusively mediotergal setae (BERTRAND, 1928). Other dytiscids additionally show at each wing base at least 2 setae; as single exceptions of their general absence in Dytiscinae, we observed in *Hydaticus transversalis* (Pontoppidan) 1 small seta at each wing base, and in a pupa of *Dytiscus dimidiatus* Bergsträsser 1 small seta at each forewing base and 2 small ones at each hindwing base. As to the loss of laterotergal setae, ref. character 7 d'.

Conclusion

That the monophyly of the Dytiscinae is beyond dispute can be confirmed by five clear synapomorphies.

Before continuing in our search of the phylogenetic position of *Lancetes*, it seems expedient to offer some comments:

1. Obviously, each of the preceding four steps of our analysis provided convincing evidence enabling us to conclude, that the group under discussion is to be considered a monophyletic unit. That is why we felt able to anticipate the evaluation of the «apomorphies common to ...» by entitling each step «synapomorphies of ...».
2. We succeeded in demonstrating that '*Lancetes* + *Colymbetinae* + *Dytiscinae*' form a monophyletic unit, and, furthermore, that each of the three groups themselves form independent taxa. The monophyly of the uniform genus *Lancetes* is beyond dispute. In such a case, three possibilities for relationships remain conceivable; but only one of them corresponds to the true phylogenetic tree.
3. Surprisingly, in analysing the three combinations, we found arguments for each of them; the possible conclusions contradict each other. Therefore we entitle the following steps «apomorphies com-

mon to ...», because a part of the derived features must be due to processes such as parallelism, convergence or secondary reduction.

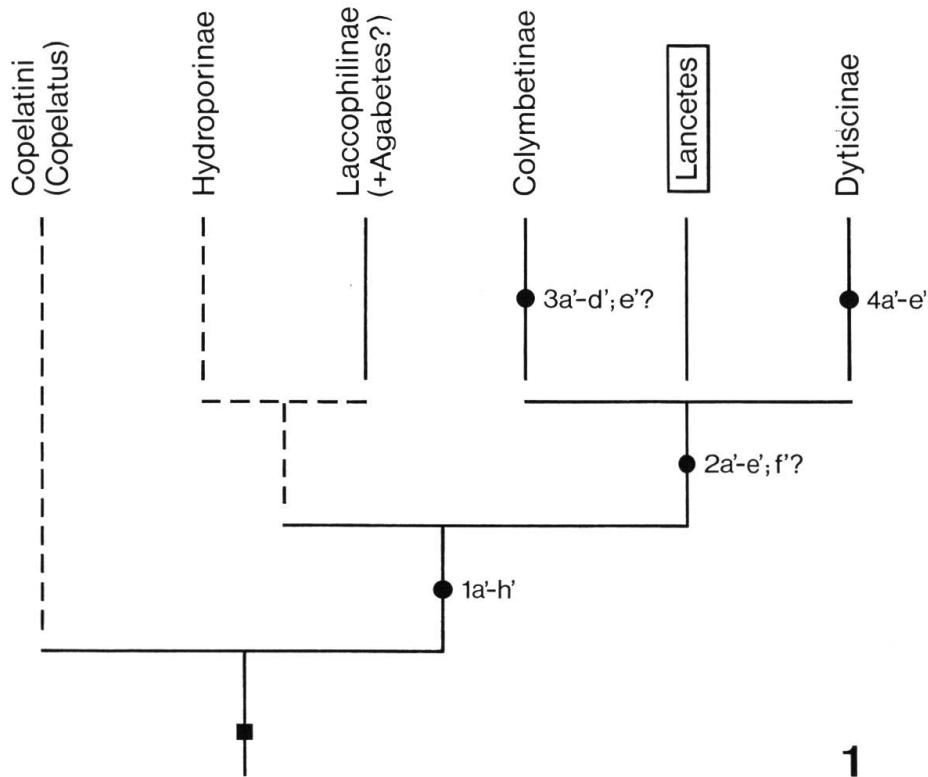


Fig. 1: Diagram of the phylogenetic relations within the Dytiscidae, as revealed by the analysis of larval and pupal characters (steps 1–4). The synapomorphies are indicated by ●. Uninterrupted lines indicate monophyletic units as evidenced in this paper; evidence for the monophyly of the family Dytiscidae (marked by ■) is given by RUHNAU (in press).

Step 5. Apomorphies common to Colymbetinae and Dytiscinae, but absent in *Lancetes*

Larvae

a'. Lateral tracheal stems considerably enlarged and laterally compressed not only in L_3 , but at least in L_2 as well

The enlarged, compressed main tracheae show at their narrow sides characteristic dark strengthenings of the spiral filaments (PORTIER, 1911: 227, 251).

So far known, all Colymbetinae show this marked development of the tracheal stems (at least in the abdomen) from L_2 on (we do not know the conditions in L_2 of *Matus* and *Coptotomus*). Dytiscinae have very enlarged main tracheae in L_{1-3} . In contrast to that, *Lancetes* and also *Copelatus* have such tracheal stems exclusively in L_3 ; this feature is markedly developed in *Lancetes*, moderately in *Copelatus*. Hydroponinae and *Laccophilus* possess tracheal stems being generally small in diameter and nearly cylindrical, at most feebly widened and compressed in L_3 . Curiously, *Agabites* although probably most closely related to Laccophilinae shows clearly enlarged and compressed abdominal tracheal stems from L_2 on (suspected convergence).

The presence or absence of markedly enlarged tracheae as early as in L_2 seems not to be directly correlated with the absolute size of a dytiscid larva; e.g. L_2 of *Agabus affinis* (Payk.), a small colymbetine larva, possesses clearly enlarged and compressed main tracheae, whereas they are narrow and cylindrical in the larger L_2 of *Lancetes*. This peculiarity seemingly led WATTS (1963) to say of *Lancetes*: «main tracheal tubes narrow», whereas in its L_3 they are markedly enlarged and compressed.

b'. Mandibular channel in the middle part of its course (nearly completely closed (from L_2 or even L_1 on)

At most a fine slit between the closing lips of this channel part remains visible; the distal channel opening is relatively narrow (DE MARZO, 1976c, 1977). In contrast to these 2 subfamilies (inclusive of *Matus* and *Coptotomus*), *Lancetes* (even in L_3) shows its mandibular channel only poorly «closed», remaining open by a rather broad slit throughout its course, and the distal channel opening is very broad (suspected plesiomorphy).

Pupae

c'. At least the anterior 3–4 abdominal terga posteriorly with a transverse crest, each

They are distinguishable in Agabini and, even better, in *Ilybius*, and in all others markedly distinct (GALEWSKI, 1963, 1964, 1966, 1967; BERTRAND, 1928). In *Lancetes*, however, a very weak crest is present solely on the first abdominal tergum. Surprisingly, in the single presently known specimen of a *Matus* pupa such crests are lacking (tergal crests do not belong to the ground-plan of dytiscids).

d'. Anterior margin of pronotum with a distinct or even markedly protruding transverse crest which is medially notched

In contrast, *Lancetes* possesses a weak crest which ascends only gently on its anterior side and has no more than an indication of a median notch. *Agabus*, which in this aspect comes nearest to *Lancetes*, has a more distinct crest, ascending much steeper than in *Lancetes*, and the median notch is distinctly visible. *Coptotomus*, which was joined together with *Lancetes* in a special tribe Coptotomini (BRINCK, 1948), has in contrast to this genus a very protruding crest and a deep, somewhat broad median notch (according to WILSON, 1923). In *Copelatus* no trace of an anterior crest is visible. Again as a surprising exception, the single specimen of *Matus* shows no pronotal crest.

The relatively weak anterior crest and median notch in *Dytiscus* must have arisen secondarily.

Conclusion

Presuming that the plesiomorphic conditions observed in *Lancetes* are not secondary developments, the 4 apomorphies presented could be interpreted as synapomorphies of 'Colymbetinae + Dytiscinae', resulting in a sister-group relationship between these and the genus *Lancetes* (Fig. 2).

Further, this hypothesis would allow the use of parsimony in explaining certain changes of pupal setation: the pupa of *Lancetes* shows no setae on the middle and sublateral area of the pronotum (BRANCUCCI & RUHNAU, in press), in contrast to a number of these setae present in the 2 subfamilies; as in the ground-plan of dytiscids presumably only very few discal setae are present (e.g. in *Copelatus* 1 pair), *Lancetes* on the one hand would have lost the few discal setae (autapomorphy), and, on the other hand, the common stem species of 'Colymbetinae + Dytiscinae' would have had a higher number of these setae (at least 3–4 pairs) (synapomorphy), when interpreting the absence of discal setae in a part of the species of *Hydaticus* and in *Thermonectini* as secondary development.

Step 6. Apomorphies common to *Lancetes* and *Colymbetinae*

Larvae

a'. Femora in L_{2-3} ventrally with two parallel rows of spiniform setae – an anteroventral and a posteroventral one – enclosing a comparatively broad, only slightly convex ventral face

Such a differentiation of the ventral femoral setae is unknown of other dytiscids, apart from somewhat similar patterns occurring in some *Hydroporinae*.

In *Lancetes*, *Agabus*, *Platambus*, and *Ilybius* the situation is as described; other, more derived genera show certain secondary changes of this basic pattern of *Colymbetinae*. In *Matus* the ventral face is somewhat narrowed, the posteroventral row of fore-femora is sparse and consists of only few small, barely spiniform setae. In *Colymbetes*, *Rhantus*, and *Meladema* on the ventral face some stiff, mostly long setae are added ventromedially, thus forming a more or less complete third, intermediate row which partly approaches the anteroventral one; in these cases the ventral face is mostly narrowed and more convex than in the primitive state. *Coptotomus* shows a strongly derived situation: the ventral face is very narrow and convex, nearly keel-like; the anteroventral row consists of a mixture of shorter and longer spines possibly reflecting the combination of the mentioned third row of longer spines with the former anteroventral one; the posteroventral row is completely reduced. These latter conditions considerably contrast to those of *Lancetes* showing an especially broad ventral face on its femora and two very well developed, distant rows of moderately long spines (cf. discussion).

In order to make plain the difference between the colymbetine-*Lancetes*-type femora and the superficially similar ones of *Agabetes*, we have to mention another peculiarity on the ventral side of femora present in various more primitive dytiscid genera, obviously belonging to the ground-plan of the Dytiscidae. *Lancetes* possesses an incomplete row of fine microspicules (BEIER, 1928) approximately parallel to and even with each of the two mentioned rows of spiniform setae. These microspicular rows become reduced within the *Colymbetinae*, but the remainder (especially of the anteroventral row) is still more or less distinguishable in the distal halves of femora of various species of some more primitive colymbetine genera (but e.g. not in *Coptotomus* and *Matus*). So far, these microspicular rows and their reductions seem to

be of little value in searching for the phylogenetic position of *Lancetes*. To return to *Agabetes acuductus* (Harris), this species possesses a relatively broad, slightly convex ventral femoral face similar to that of primitive colymbetines, bearing, however, only one sparse, more or less anteroventral row of few spiniform setae; the two parallel microspiculal rows enclosing this ventral face should not be taken for true setae⁴.

It is obvious that the colymbetine-*Lancetes*-type femoral condition is apomorphic compared with femoral conditions found in *Copelatus*, *Agabetes*, *Laccophilus*, and various *Hydroporinae*, and that it belongs to the ground-plan of 'Lancetes + Colymbetinae'. The next-related *Dytiscinae* possess femora with a ventral swimming fringe and a ventral keel (see character 4 c'). The colymbetine-*Lancetes*-type pattern is surely not derivable from such highly specialized leg conditions. However, we do not know the starting-point conditions for the evolution of the typical dytiscine pattern, which was probably still absent at the time of the origin of the *Dytiscinae* and their sister-group, but arose during the period prior to the existence of the last common stem-species of all recent *Dytiscinae*. Their fringe and keel could have arisen secondarily from the colymbetine-*Lancetes*-type pattern (cf. the strong change of this character in *Coptotomus*!), or directly from another, more primitive pattern. In other words, we cannot decide, based on leg comparisons, whether the present characteristic of recent Colymbetinae and *Lancetes* has eventually already been part of the ground-plan of the monophyletic group 'Lancetes + Colymbetinae + Dytiscinae', but lost during the evolution of the *Dytiscinae*. If this is correct, this character cannot be used for establishing a group 'Lancetes + Colymbetinae'.

b'. Antennal sensorial appendage rather strongly reduced

See character 3 b'; the strongly reduced size of the appendage in *Lancetes* may represent an advanced intermediate stage of the reduction accomplished in recent Colymbetinae.

⁴ In *Agabetes* these microspicules, especially those of the pronounced posteroventral rows, are arranged in many regular small groups, each consisting of a few, basally adjoining spinulae, as is known only for *Laccophilus* («écailles pectinées» of BERTRAND, 1928; series of «ctenidi» of DE MARZO, 1976b). However, *Laccornis oblongus* (Stephens), exceptional among the *Hydroporinae* in having retained the anteroventral microspiculal row on its fore femora as a single row, obviously shows the same modification of microspicules to «ctenidi», which may be interpreted as a synapomorphy of 'Agabetes + Laccophilus + Hydroporinae'.

Conclusion

The outlined apomorphies a' and b', if regarded as synapomorphies of '*Lancetes* + *Colymbetinae*', would suggest that they both form the sister-group of the *Dytiscinae* (Fig. 3).

Step 7. Apomorphies common to *Lancetes* and *Dytiscinae*, but absent in *Colymbetinae*

Larvae

a'. The inner one of the primary setae posteriorly on sternum VIII is secondarily very thin, small and flexible

In contrast, this seta, named V_3 by DE MARZO (1974a), is robust, very or moderately long, and thick-based in L_1 of all *Colymbetinae*, as well in L_1 of *Copelatus*, *Laccophilus* and *Hydroporinae* (plesiomorphic condition) DE MARZO, 1974a, 1974b, 1976a, 1976b). Data of *Coptotomus*- L_1 are lacking; in *Matus*- L_3 the seta V_3 is very robust, thus the condition in L_1 may be similar.

Further details: The 3 primary setae, named V_3 , V_4 , and V_5 , are situated side by side posteriorly on sternum VIII. V_4 and V_5 are developed as follows:

Copelatus, *Laccophilus*, *Colymbetinae*: V_4 : thin, flexible, hair-like, of approximately medium length. V_5 : short or very short, fine.

Dytiscinae: V_4 : a long, flexible hair. V_5 : (nearly) minute, fine.

Lancetes: V_4 : minute, fine. V_5 : robust, rather thick-based, 3 \times longer than V_3 .

In summary, *Lancetes* and the *Dytiscinae* agree in the same apomorphic change of V_3 ; concerning V_4 and V_5 , the *Dytiscinae* have only slightly changed the conditions belonging to the ground-plan of dytiscids, whereas *Lancetes* shows strong and contrary, probably autapomorphic changes.

As to *Copelatus*, V_{3-5} are situated about half-way of the distance between the beginning of sternum VIII and the cercal bases, in front or somewhat anterolaterally of the «semimembranous plate», which we tentatively homologize to sternum IX (cf. character 1 f). If it is correct to regard V_{3-5} as a characteristic marking the posterior margin of sternum VIII, the setal positions support our conclusions concerning, on the one hand, the sternum VIII of *Copelatus* as being short, followed up

by the suspected sternum IX, and, on the other hand, the caudal prolongation of sternum VIII in all dytiscids without Copelatini.

b'. Secondary changes concerning a characteristic primary coxal seta

In the plesiomorphic condition, one of the coxal primary setae is especially conspicuous and characteristically situated: it is clearly spiniform and has a separate position approximately at coxal midlength, or somewhat more distally, on the ventroanterior area, thus clearly detached from the anterior longitudinal coxal edge bearing a few setae (cf. Fig. 5 of DE MARZO, 1973, 1974a; WOLFE & ROUGHLEY, in press). This situation, markedly developed at least on mid and hind coxae, is found in *Hygrobia*, *Copelatus*, a part of the Hydroporinae (e.g. *Hydrovatus*, *Hygrotus*), and – as is of interest here – in all Colymbetinae without any exception (in *Coptotomus* this spiniform seta is typically situated on all its coxae, but is relatively thin as are many of its other spines).

In both *Lancetes* and all Dytiscinae this seta while having become thin and small is shifted very far to the proximal end of the coxa (synapomorphy?). At first we thought that this seta would be entirely lacking, but extensive comparisons throughout the Dytiscidae revealed the present interpretation, because dytiscid coxae obviously show a constant number of 18 primary setae, of which most are distributed in a nearly invariable pattern. Similar changes in the position of this characteristic seta can also be observed in *Laccophilus* and in some more derived genera of Hydroporinae (parallel developments).

c'. Quality of swimming hairs of the same kind

The long, very dense and fine fringes of swimming hairs dorsally on the tarsi and tibiae in L_{2-3} of *Lancetes* conspicuously resemble those of the Dytiscinae (BEIER, 1928; BRINCK, 1945, 1948).

In the more primitive genera of Colymbetinae (e. g. *Platambus*, *Agabus*, *Ilybius*; *Senilites*, BRINCK, 1948), swimming hairs are generally absent, except for the relatively few and short ones occurring in few species of *Agabus* (s. l.). Other, more derived colymbetine genera as e.g. *Coptotomus*, *Matus*, *Colymbetes*, *Rhantus* or *Meladema* show moderately dense dorsal fringes of swimming hairs, but they are never so fine and dense as those seen in *Lancetes* and the Dytiscinae. However, a convergent development of such fine, dense swimming hairs in *Lancetes* and in the Dytiscinae cannot be excluded.

Pupae

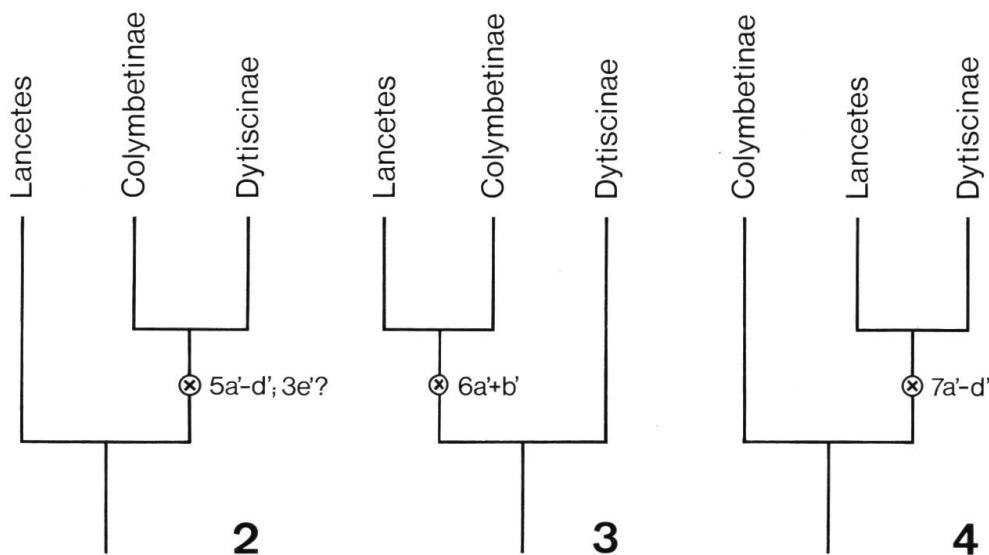
d'. Meso- and metanotum without laterotergal (anterolateral) setae

In contrast to this, all Colymbetinae (incl. *Matus*) possess 1–2 pairs of setae in this position, rarely more (*Meladema*). So far, as a unique exception within the Colymbetinae, we observed the lack of these setae in a pupa of the Nearctic *Agabus disintegratus* Crotch, in contrast to their constant presence in a number of other species of *Agabus* examined by us and by BERTRAND (1928). Conditions in other dytiscid groups are as follows: *Copelatus* has 2 pairs on mesonotum and 0 on metanotum (SPANGLER, 1962, and our results). The Hydroporinae have usually 1 pair on both meso- and metanotum, rarely 0 (*Hygrotus*, *Graptodytes*); and *Laccophilus* lacks these setae (BERTRAND, 1928).

A convergent reduction in *Lancetes* and in Dytiscinae cannot be ruled out (cf. character 4 e').

Conclusion

The outlined four apomorphies, if regarded as synapomorphies of 'Lancetes + Dytiscinae', would suggest that they both form the sister-group of the Colymbetinae (Fig. 4).



Figs 2–4: Possible relationships amongst Lancetes, Colymbetinae and Dytiscinae. Each solution of the three possible sister-group relationships can be supported by a few, so far uncertain (syn)apomorphies (cf. steps 5–7), as indicated in the respective diagram by \otimes . Provided the dendrogram in figure 1 is correct, only one of the solutions does reflect the actual relationships.

III. Discussion

Since many comments are given throughout the analysis, we focus the final discussion on the following points:

- What results argue against the hitherto accepted phylogenetic position of *Lancetes* as being in a special tribe Coptotomini within the Colymbetinae, and also support our conclusion that a group ‘Colymbetinae excluding *Lancetes*’ is monophyletic (A).
- What conclusions may be drawn concerning the sister-group relationships amongst *Lancetes*, Colymbetinae, and Dytiscinae (steps 5–7) (B).
- What are the main results (C).

A. BRINCK (1948) has linked *Lancetes* with *Coptotomus* in a special tribe Coptotomini, emphasizing the similarity of their parameres. Apart from a number of deep differences between the larvae and pupae of these two genera, we also observed some surprising similarities: labrum of L_1 with an unusual 4-peg-pattern (cf. step 2), larval antennae with a sensorial appendage (cf. character 3 b’), and spiracles of L_3 situated in the pleural membrane (cf. character 3 d’). However, the following look at various strong differences between *Coptotomus* and *Lancetes* will expose the above similarities as most likely independently developed features:

1. *Lancetes* possesses very small, roundish presternite plates, probably smaller than in any species of *Agabus*, *Platambus*, or *Ilybius*; these plates are developed as narrow, transverse, stripe-shaped sclerites in *Matus*, and as large and long ones in *Coptotomus* (even larger than in Colymbetini s. str., already similar to dytiscine conditions, but without being fused medially) (cf. character 2 b’).
2. The femoral basic pattern of colymbetines is present in *Lancetes* in a very primitive state, whereas the femoral condition of *Coptotomus* is strongly derived (cf. character 6 a’).
3. *Matus*, *Coptotomus*, and the Colymbetini s. str. possess an elongated maxillary galeal joint (proportion of length: breadth, without subgalea, at least 3.5: 1; possible synapomorphy), in contrast to a short galea seen in *Lancetes* (proportion 2: 1). Few species of *Agabus* and *Ilybius* have galeae as short as that of *Lancetes*; the usual proportion value in these genera is approx. 2.5: 1.

4. The first labial palpal joint is only slightly longer than the second one in *Lancetes*, however considerably prolonged in *Coptotomus*, *Matus*, and others (cf. character 2 c').
5. *Lancetes*, although having extremely well-developed swimming fringes dorsally on its tibiae and tarsi (character 7 c'), lacks any swimming hairs on its femora. *Matus* (WOLFE & ROUGHLEY, in press), *Coptotomus*, and the Colymbetini s. str. agree in having swimming fringes dorsally on their tarsi, tibiae, and, moreover, on their femora (presumable synapomorphy).

In summary, it is obvious that *Lancetes* possesses the listed characters in a primitive state, in contrast to their clearly derived conditions seen in *Coptotomus* and many other colymbetines. Adding this evidence to that of those characters presented in steps 3 and also 5, our conclusion appears justified that a group 'Colymbetinae excluding *Lancetes* (and without *Agabetes* and *Copelatini*)' form a monophyletic group. Thus some peculiar deviations of the rule of single characters in *Coptotomus* or *Matus* are obviously due to secondary events.

B. In the steps 5–7 of our analysis we tested each of the remaining possible relationships amongst *Lancetes*, Colymbetinae, and Dytiscinae. The surprising result is that arguments can be made for each of the three possible solutions of sister-group relationships; however, only one solution reflects the actual relationships (Figs 2–4).

Let us again review the observed possible «syn»apomorphies. Admittedly, none of the various outlined apomorphies seems to be of such a uncontestable quality as to make it highly credible as having been derived «only once».

Thus the four arguments listed in step 5 (*Lancetes* as «sister» of the others) indeed demonstrate that *Lancetes* possesses some characters in a clearly more primitive state than all the others; however, such «strengthenings» of previously introduced evolutionary trends as observed in Colymbetinae and Dytiscinae could be due to an evolutionary event that occurred «only once», but also to a parallel development.

The arguments 6 a' (ventral femoral pattern) and 6 b' (antennal appendage becoming reduced) are the only two apomorphies we could find that are common to *Lancetes* and Colymbetinae, but absent in dytiscines. They could indeed be true synapomorphies, but it remains uncertain, first, whether the colymbetine femoral pattern eventually had been present in early Dytiscinae prior to the strong specialisations of their legs for swimming, and, second, whether the trend to a strong reduction of the antennal appendage arose only once.

The four arguments of step 7, seemingly linking *Lancetes* directly with the Dytiscinae, concern some minor changes of certain setal conditions, and the quality of swimming fringes. Parallel development in these characters is imaginable.

If *Lancetes* would be the sister-group of all (other) Colymbetinae, then both statements that 'Colymbetinae excluding *Lancetes*' and that 'Colymbetinae including *Lancetes*' are monophyletic would be correct. In this case *Lancetes*, which we treated separately throughout the analysis for methodological reasons, would represent the monogeneric first primitive side-branch within the whole subfamily Colymbetinae.

Further studies on the «tendon plate» (character 3 e') would eventually reveal that the long-tendon-condition seen in 'Colymbetinae excl. *Lancetes*' and in Dytiscinae arose only once, thereby pointing for one of the other two possible solutions: *Lancetes* as the sister-group of both subfamilies.

A judgement considering this situation in light of conflicting evidence would be risky; further studies are clearly called for before a definitive statement can be made.

C. *Lancetes* is in many characters very primitive. SHARP (1880–82), studying adult characters, already hesitated about a placement of the genus within the Colymbetinae and ranged it among his group «7 unrelated genera». BEIER (1928), stressing some larval peculiarities of *Lancetes*, likewise called in question its usual assignment to the Colymbetinae. The present analysis can confirm this particular position of *Lancetes*, and, moreover, makes clear that some other genera, hitherto ranged among the Colymbetinae, actually do not belong to this subfamily.

The analysis provides the following main results:

1. *Copelatus* is in many characters undoubtedly more primitive than *Lancetes* and even all the other dytiscids. We evidenced a sister-group relationship between *Copelatus* (with its allied genera) and the clearly monophyletic group 'Dytiscidae incl. *Lancetes* without Copelatini' (step 1).
2. 'Lancetes + Colymbetinae (excl. *Agabetes*) + Dytiscinae' form a monophyletic unit (whose sister-group might be the group '*Agabetes* + Laccophilinae + Hydroporinae') (Fig. 1). Characteristic novelties are the presternite plates, and the intercercal sclerite with its muscle connection to the lateral base of each cercus (step 2).
3. The 'Colymbetinae excl. *Lancetes*', and the Dytiscinae are

monophyletic groups, as shown by several synapomorphies in both cases; the genus *Lancetes* is surely monophyletic.

4. The problem of the three remaining possibilities of relationships between the three groups could not be resolved (steps 5–7; Figs 2–4). So far, our search for credible preimaginal synapomorphies which would speak for one of the possible solutions provided nothing but conflicting evidence by characters of unclear credibility as having been arisen «only once».

Finally, a knowledge of the correct phylogenetic position of *Lancetes* would be interesting for zoogeographical considerations: *Lancetes* is the only dytiscid genus with a predominantly far-southern, transantarctic distribution pattern (cf. distribution map in BRINCK, 1945).

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