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On the primitive and derivative characters of the families of beetles (Coleoptera)

The student may refer to CAIN & HARBISON (1960) and SIMPSON (1961) for understanding the principles of phyletic weighting and the theoretical background of this paper. These will not be discussed here. The classification of beetles (Coleoptera) and the arrangement followed here is the same as outlined by ABDULLAH (1969b). Usually only one, primitive (P) or derivative (D), alternative of a distinguishing character is mentioned below for the sake of brevity.

According to CROWSON (1955), the primitive or original Coleopteron probably evolved in the Permian and had the following features:

 9 or 10 regular striae and a scutellary striole in the elytron (P).
 Creeping under close fitting bark with special type of longitudinal ribbing and particularly the development of a convex yet flattened and elongate elytron (P).

3. Adult legs short (P). 4. Femoral plates on the hind coxae as in Dascillidae, etc. (P).

5. A transverse suture on the metasternum as in Carabidae, Dascillidae, Dryopidae, etc. (P).

6. 2 or 3 dorsal ocelli (P)

7. Hind wings with the apical part spirally rolled in repose as in Archostemata (P). 8. Larval legs of the Caraboid pattern (P).

 Darvae with articulated cerci or urogomphi (P).
 Larvae mouth parts of the type found in such families as Anisotomidae or Hydraenidae (P).
 Mould-eating habits of the larvae in view of the primitive mouth parts and the adaptations of the adults (P). SMITH (1950) from his studies on the cytotaxonomy of the Coleoptera concludes a chromosome complement

of 9 pairs of autosomes and an XY sex-determining pair, the sex-chromosomes in spermatogenesis forming a characteristic parachutelike figure as features of the primitive beetle (P).

The morphological characters of adults and larvae of the families and other groups are arranged under the heading 'head', 'thorax' and 'abdomen'. Other characters are analysed towards the end under the heading 'miscellaneous characters' (vide infra). Additional research is needed in case of many families of the Coleoptera. Important phylogenetic conclusions (vide CROWSON 1955 and 1960, ABDULLAH 1964-1969, and ABDULLAH & ABDULLAH 1966-1968) on the primitive or derivative alternative of the distinguishing characters of the families and other groups of the Coleoptera follow:

Head

Distinct labrum in larva in Rhysodidae (= Rhyssodidae) (P). Groove on upper surface of head in Rhysodidae Distinct labrum in larva in Rhysodidae (= Rhysodidae) (P). Groove on upper surface of head in Rhysodidae (D). Prognathism, loss of mandibular mola, hypopharyngeal sclerome in larva in Adephaga (D). Adult mandibular scrobe without seta in Caraboidea (D). Antennae moniliform in Paussidae (D). Larval mandibles unchanelled in Hygrobidae (= Pelobidae) (P). Antennae clubbed in Myxophaga (D). Mandibles with a distinct mola and with a supplementary articulated tooth behind the normal apical one in Myxophaga (D). Maxillae without distinct galea in Myxophaga (D). Larval mouth parts: mandibles with a basal molar part and more or less articulated retinaculum (lacinia mobilis), maxillae with well-developed galea and lacinia and large articulating area, and labium bearing a hypopharynx with distinct paragnathal structures in Polyphaga (P). Larval mandibles falcate, larval maxillary galea displaced to lie on an elongated palpiger in Hydrophilidae (= Helopheridae or Sphaerididae) (D). Palpicorn antenna in Hydraenidae (= Limmebiidae) and Hydrophilidae (P). Adult with 2 ocelli in segmenta a tyricai (cupule and a 5-segmented loose pubescent club in Hydraenidae (P). Adult with 2 ocelli in (D). Palpicorn antenna in Hydraenidae (= Limnebidae) and Hydrophildae (D). Antennae with 5 basal glabrous segments, a typical cupule and a 5-segmented loose pubescent club in Hydraenidae (P). Adult with 2 ocelli in Hydraenidae (P). Larval maxillae without galea, lacinia rudimentary; larval mandible with large retinaculum, mola small in Hydrochidae (D). Antennae with segment II and cupule pubescent, latter effectively part of club in Spercheidae (D). Maxillary palpi shorter than antennae in Georyssidae (D). A V-shaped impressed line on vertex in Hydrophiloidea (P). Prognathism, labrum fused into nasale, mandibles falcate, palpiger clongate in Histeroidea (D). Gular sutures separate in Syntellidae (P). 2 dorsal ocelli in adult in some Staphylinoidea (P). Antennae with segments IX and X with small round internal vesicles in Leptinus, Leptinidae, Anisotomidae (- Anteidae or Loicdidae) and Entheig Soudmennidae (D). Larvae with peculiar finges a part of maxillary Antennae with segments 1X and X with small round internal vesicles in *Leptinus*, Leptinidae, Anisotomidae (= Agathidae or Leiodidae) and *Butheia*, Scydmaenidae (D). Larvae with peculiar fringes at apex of maxillary mala in Anisotomidae and Ptillidae (P). Clypeus with deep membrane-filled emargination in *Nicrophorus*, Silphidae (= Agyrtidae or Necrophoridae) (D). 2 dorsal ocelli, antennae filiform in *Brathinus*, Scydmaenidae (P). Maxillary palp with preapical segment III very large in Scydmaenidae (= Anisosphaeridae) (D). Eyes entire in *Scaphium*, Scaphidiidae (P). Larval madible with prostheca in Omalinae and Proteininae, Staphylini dae (P). 5 or 6 larval ocelli in Paederinae, Staphylinidae (P). Mentum entire in Lucanidae (P). Maxillary galea with a chitinous hook at apex in Passalidae (D). Larval antennae 4-segmented in Acanthoceridae (P). Antennae Lesemented in Trovidae (P). Antennae 10-segmented labrum and mandible without very soed in Scarahadidae 11-segmented in Trogidae (P). Antennae 10-segmented, labrum and mandibles distinctly exposed in Scarabaeidae (P). Larvae with distinct lateral ocelli in Cetoniinae, Scarabaeidae (P). Larval antennae long, multiarticulate in Helodidae (= Cyphonidae) (D). Larval mandibles with a ventral crushing tubercle and a rigid retinaculum in Heteroceridae (D). Antennae strongly pectinate or flabellate, inserted close together on a protuberance of front of head; labrum nasale-like, projected in Rhipiceroidea (D). Antennae 12-segmented in Rhipicerini, Rhipiceridae

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(D). Larval labrum free in Buprestidae and Eurypogonidae (P). Larval mandibles outwardly biting in Trixaginae, Trixagidae (= Throscidae) (D). Larval mouth parts reduced, digestion extraoral in Eucnemidae (= Eucnemididae, Melasidae or Phylloceridae) (D). Larval mandibles with inner surface chanelled or longitudinally perforate in Cantharoidea (D). Labrum fused with clypeus in Karumiidae (= Zarudniolidae) (D). Larvae without epicranial suture in Drilidae (= Rhagophthalmidae) (D). Larval maxillary stipes free, carde absent in Drilidae (D). Antennae 12-segmented and strongly plumose in male in Phengodidae (D). Antennae in approximate of their sockets dorsal in Cantharoidea (D). Eyes in male very large, divided by a horizontal canthus into two halves with different sized ommatidia in Rhagophthalminae, Lampyridae (D). Antennae 11-segmented in Lampyridae (P). 2 dorsal ocelli in Derodontidae (= Laricoblidae or Peltasticidae) (P). Antennae insertion ayeinae, (D). Antennae io-segmented in Gaotus and 9-segmented in Ptinuxs, Ptinidae (= Gnostidae or Estrephidae) (D). Antennae io-segmented in Gaotus and 9-segmented in Ptinuxs, Ptinidae (= Gnostidae or Estrephidae) (D). Antennae io-segmented in Corynetinae, (P). Larval maxilla with apical lobe partially divided in Ptinuxs, Ptinidae (D). Antennae theoremus, Melyridae (P). Larval maxilla with apical lobe partially divided in Lymexylidae (D). Antennae weakly clubed, inserted laterally in front of eyes in Caucijoidea (P). Larvae with frontal and prostheca in Cucujoidea (P). Larval and free labrum in Cucujoidea (P). Larvae with well-developed articulating area, mala probably long and acute, papi 3-segmented (excluding palpiger) in Cucujoidea (P). Larval maxillary lobes to 1 in Nitidulidae, Corylophidae, Lathrididae and Ptillidae (D). Antennae (D). Larvae with nort astillary lobes to 1 in Nitidulidae, Corylophidae, Lathrididae and Ptillidae (D). Eves entire as in Neopedilus ABDULLAH, Steropes, Macratinae, Copobaenus, most Eurygeniinae and Anthi-cinae of Anthicidae, also in Techno

Thorax

Elytra sculptured with scutellary stricle in Cupedidae (= Cupesidae or Ommatidae) (P). Groove on upper surface of prothorax in Rhysodidae (D). Antenna cleaning apparatus of front tibiae in Caraboidea (D). Extension of inner apieal angles of mes-episterna to reach middle coxal cavities in Caraboidea (D). Reduction of tarsal claws from 2 to 1 in Caraboidea (D). Open front coxal cavities in Caraboidea (D). Bordered bases of elytra in Caraboidea (D). Non-swimming legs in Amphizoidae (P). Met-episternum reaching middle coxal cavities in Amphizoidae (D). Non-swimming legs in Amphizoidae (P). Met-episternum reaching middle coxal cavities in Hydroporidae (P). Tarsi with reduced number of segments, none of them lobed; prothorax with distinct notopleural sutures; hind wing with oblongum cell in Myxophaga (D). Prothorax without onlopieural sutures in Polyphaga (P). Hind wing without oblongum cell in Myxophaga (D). Prothorax without on uside of water surface (in misgentraide (D). Tarsi 4-4-4 segmented in Georyssidae (D). Front coxae very large, concealing sternum in Georyssidae (D). Larvae terrestrial and without legs in Gereyon, Hydrophilidae (D). Met-endosternite or furca with distinct median stalk nearly as long as lateral arms, anterior tendons arising close together on a median projection In Sphaeritidae (D). Tarsi 5-5-4 in some Histeridae (D). Hind wing without a *m-eu* loop in Staphylinoidea (D). Elytar turnaca in Pililidae (C) Legs with hind coxae mobile and hind border of metasternum emarginate in Staphylinidae (D). Hind coxae projecting and elytra without episelural keel in Staphyliniae and Paederinae, Staphylinidae (D). Hind coxae mobile and hind border of metasternum ear in staohodiae (P). Hind wings with 5 anal verias and anal (= wedge) cell in Staphyliniae and Agederinae, Staphylinidae (D). Hind coxae the sind anal (= wedge) cell in Staphyliniae and Agederinae, Staphylinidae (D). Hind coxae the sind and anal (= wedge) cell in Staphyliniae and Buprestidae (P). Mind coxae (P). Hind wings with 5 anal verias

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welldeveloped in Corynetinae, Cleridae (P). Tarsal claws simple in Acanthocnemus, Melyridae (P). Tarsal formula 4-5-5 in male in Melyridae (D). Transverse front coxae with exposed trochantins in Cucujoidea (P). Middle coxae with exposed trochantins in Cucujoidea (P). Middle coxae strongly transverse and nearly contiguous in Cucujoidea (P). Tarsi with 5 normal segments, at least in female in Cucujoidea (P). Mid-endosternite of Hylecoetoid type with anterior tendons close together in Cucujoidea (P). Elytra completely covering abdomen, probably more or less striate and with a scutellary striole in Cucujoidea (P). Larval legs of normal Polyphagan type in Cucujoidea (P). Truncate elytra in Nitidulidae (P) (P). Tarsal stat-4-4 in Nitidulidae (D). Tarsal formula 5-5-4 or less in Heteromera (D). Tarsal claws pectinate in Alleculidae (P). Front coxae levities open in Hypocopridae (P). Throne of produce and Protomelee, Meloidae (P). Hind wings with radial and anal cells and 5 anal veine in Discolonidae (= Aphaenocephalidae or Notiophygidae) (D). Front coxae projecting in Heteromera (D). Tarsal formula 5-5-4 or less in Heteromera (D). Tarsal claws pectinate in Alleculidae (P). Front coxae completely enclosed by sterna in Discolonidae (P). Tarsal claws appendiculate in Pyrochroidae (P). Front coxae and earlied end completely (externally and internally) open as in Pedilinae, and Steropinae of Anthicidae, also in Aderidae, Meloidae, Meloidae and Cephaloidae (P). Front coxael and Cephaloidae (P). Hind wing with radial and anal cells prochroidae, and centrine, Source, Steropinae, Copobaeninae, Macratrinae, Loubacantus etc. of Anthicidae, also in Aderidae, Pyrochroidae, Meloidae and Cephaloidae (P). Hind wing with radial and anal cells present as in Pedilinae, Steropinae, Macratrinae, some Eurygeninae of Anthicidae, also in anthicidae (P). Hermitoxicae, Steropinae, Copobaeninae, Macratrinae, Loubacantus etc. of Anthicidae, also in Aderidae, (P). Tarsal claws appendicula

Abdomen

Urogomphi absent in larva in Rhysodidae (D). Aedeagus without a basal piece in Hydraenidae (D). 6 or 7 visible abdominal sternites in Hydraenidae (P). First two visible abdominal sternites connate in Georyssidae (D). Aedeagus with parameres not completely fused in Sphaeritidae and Histeridae (P). Abdominal tergites selerotized except first two in Sphaeritidae and Histeridae (P). Larvae with articulated urogomphi in Staphylinoidea (P). Haplogastran abdomen with segment VIII exposed in Staphylinoidea (P). Spiracles on abdominal segment VIII exposed in Staphylinoidea (P). Aedeagus trilobe, parameres separate, basal-piece absent in Staphylinoidea (P). One or more basal abdominal tergites membranous in Staphylinoidea (P). Ninth sternite represented by a spiculum gastrale in Anisotomidae (D). Abdomen with second tergite membranous in Omalinae and Proteininae (Staphylinidae) (P). Larva without urogomphi in Micropopildae (D). Larve with cribriform spiracles and without articulated articulated urogomphi in Scarabaeoidea (D). Aedeagus with lateral lobes reduced or fused in Passalidae (D). Aedeagus with lateral lobes large and free, median lobe fully sclerotized in Trogidae (P). Abdomen with most tergites membranous in Trogidae (P). Long ovipositor in Bostrychoidea (P). Aedeagus with lateral lobes separate in Lyctidae (P). Aedeagus with lateral lobes not really articulated at base in Cleroidea (P). Pleural sclerites in second segments in Melitdomma and Lymezylon, Lymexylidae (P). Five free and visibe sternites in Caujoidea (P). Aedeagus of Cucujoid type in Cucujoidea (P). Aedeagus with main part of median lobe short and attached to basal-piece and a long secondary sclerotization (sipho) developed inside t in Coccinellidae (D). Aedeagus of inverted Heteromera (D). Appendages absent in male in Anthicidae (P). Aedeagus with parameres (= lateral lobes) separate apically in Anthicidae, Pyncehroidae and Meloidae (P). Aedeagus with parameres (= lateral lobes) separate apically in Anthicidae, Pyncehroidae and Meloidae (P

Miscellaneous Characters

Predacious mode of life in Adephaga (D). Myrmecophilous mode of life in Paussidae (with antennae consolidated to act as handles by which ants carry them about) (D). Black colour and nocturnal habit in Cicindelinae (T). Gillrespiration of larva in Hygrobildae (D). Larval habit of tapping air-spaces in water plants for oxygen in Noteridae (D). Life on still pools (Gyrinus) and running waters; adults large, broad, flat, smooth above, nocturnal (Orectochilus), Gyrinidae (D). Dull green living on densely tree-shaded waters of Amazon basin (Enhydrus), Gyrinidae (P). Larval food filamentous algae instead of moulds in Hydrophiloidea (P). Antennae used to break surface film of water to establish contact between atmosphere and an air film held by hydrofuge pubescence over ventral body surface in Hydrophiloidea (P). Larvae predacious in Hydrophiloidea (D). Adult with dorsal surface very smooth and convex, and ventral surface flattened in Hydrophiloidea (D). Small size in Scarabacoidea (P). Larval legs with stridulatory mechanism in Lucanidae (= Sinodendronidae (D). Small size in Scarabacoidea (P). Larval legs with stridulatory mechanism in Lucanidae (= Sinodendronidae (D). Justron respiration in Elmidae (= Helmidae or Limnidae) (D). Females larviform in Cantharoidea (D). Luminous organs in Lampyridae and Phengodidae (D). Highly distasteful, model for mimics, Lycidae (D). Sexual dimorphism and larviform females in Lycidae (D). Myrmecophilous mode of life in Thorictus, Thorictidae (D). Myrmeco-

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philous mode of life in Gnostus, Ptinidae (D). Predacious mode of life in Cleroidea (P). Sexual dimorphism in Lymexylidae (D). Cryptonephridic Malpighian tubules in Lymexylidae (P). Seven pairs of abdominal spiracles in Cucujoidea (P). Cryptonephridic Malpighian tubules in Cucujoidea (P). Larvae with thoracic and abdominal segments with well-marked sclerotized tergites in Cucujoidea (P). Larvae with 9 pairs of functional spiracles in segments with weil-marked sciencitized tergites in Cucujoidea (P). Larvae with 9 pairs of functional spiracies in Cucujoidea (P). Insects of loose bark and dead trees in Cucujoidea (P). Ectoparasitic degeneration of larvae in Passandridae (D). Larvae in fungal fruit bodies in Melandryidae, Erotylidae and Cisidae (P). Highly degenerate ectoparasitic larvae in Colydiidae (D). Advanced drought-resistant physiology in Tenebrionidae (D). Larvae hypermetamorphic in Rhipiphoridae and Meloidae (D). Seven pairs of abdominal spiracles in Chrysomeloidea (and other Cucujiformia) (P). Midgut entirely re-constituted in pupa in Chrysomeloidea (and other Cucujiformia) (P). Cryptonephridic Malpighian tubules in Chrysomeloidea (and other Cucujiformia) (P). Dead wood habitat for larvae in Chrysomeloidea and Curculionoidea (P). Proventriculus absent in Curculionoidea (P).

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Summary

Phylogenetic conclusions on the primitive or derivative alternative of the distinguishing morphological and other characters of the families and other groups of the Coleoptera are given.

Zusammenfassung

Es werden phylogenetische Schlußfolgerungen auf die ursprüngliche oder abgeleitete Alternative der morphologischen und anderen Unterscheidungsmerkmale der Familien und anderen Gruppen von Coleopteren gezogen.

Резюме

Даются филогенетические выводы о первоначальной или производной алтернативы морфологических и других отличительных признаков семейств и других групп жёсткокрылых.

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