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Ceratogarra, a genus name for *Garra cambodgiensis* and *G. fasciacauda* and comments on the oral and gular soft anatomy in labeonine fishes (Teleostei: Cyprinidae)

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Abstract. *Ceratogarra* is established as genus name for *Garra cambodgiensis* and *G. fasciacauda*. Besides molecular characters, *Ceratogarra* shares with *Paracrossochilus* the presence of a large tubercle on each side of the tip of the snout, the colour pattern made of a bold black midlateral stripe and a red to black marginal or submarginal stripe along the upper and lower margins of the caudal fin. It is distinguished from *Paracrossochilus* by the presence of a gular disc. The oral and gular morphology of *Paracrossochilus* is described. The difference between lower lip and labial fold is discussed. The terminology used to describe the gular disc is reviewed and a new terminology is proposed. Conclusions of recent works on garra lineages are discussed, among others the homology of soft oral and gular structures and the reduction and absence (vs. loss) of the gular disc. While the absence or small size of the disc might result from loss or reduction in some species or lineages, there is no reason to accept a hypothesis that the presence of a structure as complex as the gular disc would be the plesiomorphic condition for the whole clade 'Labeonini minus Labeonina', followed by loss of the disc and followed by the evolution of new, different, very complex structures. It is at least equally parsimonious (and more logical) to hypothesise a simple structure as plesiomorphic, followed by the evolution (including parallel) of various complex modifications of the gular tissues, including discs (which develop in different ways). The putative homology between the disc of garras in separate lineages should be critically re-examined and genera within Garrina should be diagnosed by other characters than simply by a trivial statement of the presence or absence of the disc. The gross oversimplification (or misrepresentation) of 'morphology', and even its terminology, is a serious problem in many molecular phylogenetic studies.

Key words. Labeonini, Garrina, gular disc, sucking disc

INTRODUCTION

Garras are cyprinid fishes characterised by the presence of a gular disc (also called by various authors 'labial suctorial disc', 'mental adhesive disc' or 'oral adhesive disc'). The disc had been identified as the modified posterior part of the lower lip (sensu Matthes, 1963) or of the labial fold (sensu Reid, 1985) or developed from tissues of the gular region (Minzenmay, 1933; present study). Based on African species of *Garra*, Matthes (1963) considered that adductor muscles can be contracted to pull the central part upwards, creating a suction when the disc is against the substrate; this would allow the fishes to adhere to rocks and stones and maintain their position in fast flowing water (he did not provide information on which muscles this would be). For a long time all cyprinid species with a gular disc had been placed in the genus *Garra*, a genus diagnosed mainly by the presence of this disc. They were treated as the subtribe Garrina of the tribe Labeonini of the subfamily Cyprininae of the family Cyprinidae. Species of garras are found in Africa, and Southwest, South, Southeast and East Asia. Species of *Garra* in South, Southeast and East Asia are found in habitats with strong current, such as rapids, torrents and waterfalls, usually solitary under rocks or among stones and boulders. Most have a dull brown to black body with more or less distinct darker stripes between scale rows on the posterior half of the body.

Garra cambodgiensis (Fig. 1) and *G. fasciacauda* (Fig. 2), two species from mainland Southeast Asia (Kottelat, 1998, 2001, 2013), are among the few exceptions in having a conspicuous colour pattern made of a broad, contrasted dark brown to black midlateral stripe on a pale brown background and whitish to yellow lower half of flank, and brown to reddish bands along the upper and lower edges of the caudal fin. Also, they are present in a wide variety of habitats from slow flowing streams in lowland and foot hills to fast flowing streams, but rarely in strong currents. *Garra cambodgiensis* is usually abundant; the adults live in loose groups of 4–10 individuals while juveniles 30–40 mm SL may form loose schools of tens of individuals. *Garra cambodgiensis* and *G. tenuicauda* uniquely share, among disc-bearing garras, the presence of a pair of large tubercles directed laterally near the tip of the snout. They have long been thought to be closely related to each other and somehow distinctive

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Fig. 1. *Ceratogarra cambodgiensis*, CMK 23487, 118.3 mm SL; Laos: Mekong drainage: Xe Kong watershed: Xe Namnoy.

among *Garra* sensu lato, a hypothesis now supported by molecular studies.

This article is dedicated to the memory of Tony Whitten, friend and strong catalyst of biodiversity exploration in Southeast and East Asia. By his great interest in aquatic biodiversity, Tony is directly and indirectly responsible for many large-scale fish surveys in Indonesia, Laos, Myanmar and Mongolia, which led to the discovery of more than 150 species of fish new to science. He was an advocate for aquatic biodiversity in numerous development projects. Tony was a strong promoter of field guides and he has been the driving force to the publication of books on the fishes of Indonesia (which he co-authored), Laos, Vietnam and Mongolia, and on many other groups of animals and plants.

MATERIAL AND METHODS

This study is based on preserved material as well as on large numbers of individuals observed in the field and in markets in Laos, Thailand, Vietnam and Myanmar. Preserved material is in: CMK, collection of the author; and ZRC, Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore. Spelling of scientific names, authorship and year of publication of South and Southeast Asian taxa follow Kottelat (2013), who also provides lists of synonyms, complete bibliographical references, and discussion of nomenclatural issues.

Garra is the genus name while garra (plural garras) is used as a vernacular name for the genera sharing the presence of a gular disc or those closely related to them; garra is purely a convenient term used here to facilitate discussion and does not imply phylogenetic relationships. Some members of the genera of garras do not have the disc or have been hypothesised to have secondarily lost it. Garra genera mentioned here are: *Garra*, *Ageneiogarra*, *Placocheilus*, *Sinigarra*, *Vinagarra*, *Discogobio* and *Discocheilus*.

The identification of the elements of the gular disc partly follows Zhang et al. (2002) (followed, e.g., by Nebeshwar & Vishwanath, 2017, Stiassny & Getahun, 2007), but the terminology is revised, see under Discussion and Fig. 3. The main terms used here are pulvinus (central pad or central callous pad of authors), torus (anteromedian fold of authors), labrum (lateroposterior flap of authors) and labellum (anterolateral lobe of authors).

'Semilabeonina' and 'osteochilina' are two names used for subtribes by Yang et al. (2012). These names are not available as they are not formed as prescribed by the International Code of Zoological Nomenclature. They are used here informally, within quotation marks and with a lower case initial.

TAXONOMY

Ceratogarra, new genus

Type species. *Cirrhina cambodgiensis* Tirant, 1884.

Etymology. The name is formed on the classical Greek noun *κέρας, -ατος* (keras, keratos) meaning horn, and the genus name *Garra*; it is an allusion to the two 'horns' at the tip of the snout. Gender feminine.

Diagnosis. *Ceratogarra* is distinguished from all other genera of garras by the combination of the presence of a pair of large conical tubercles at the tip of the snout, directed laterally; the numerous tubercles on the top and side of the snout (between the tip and the eye), all conical, of various sizes (Fig. 4); a broad, contrasted dark brown to black midlateral stripe on a pale brown background and whitish to yellow lower half of flank; a red to black marginal or submarginal band along the upper and lower edges of the caudal fin; a single pair of barbels (maxillary); the pulvinus of the gular disc thin, flat, covering the posterior edge of the torus (Fig. 5); the absence of groove between the pulvinus and the labrum; the lateral extremities of the torus continuous with the labrum and the labella; the labrum connected to the rostral cap by the labella (which are partly folded under the labrum in *C. cambodgiensis*); the torus, labella and labrum (sometimes also the anterior edge of the pulvinus)

Fig. 2. *Ceratogarra fasciacauda*; **a,** CMK 21299, 93.3 mm SL; Laos: Mekong drainage: Xe Kong watershed: Xe Pian; **b,** CMK 23089, 51.5 mm SL; Laos: Mekong drainage: Xe Bangfai watershed; **c,** CMK 23534, 49.7 mm SL; Laos: Mekong drainage: Nam Ngum watershed.

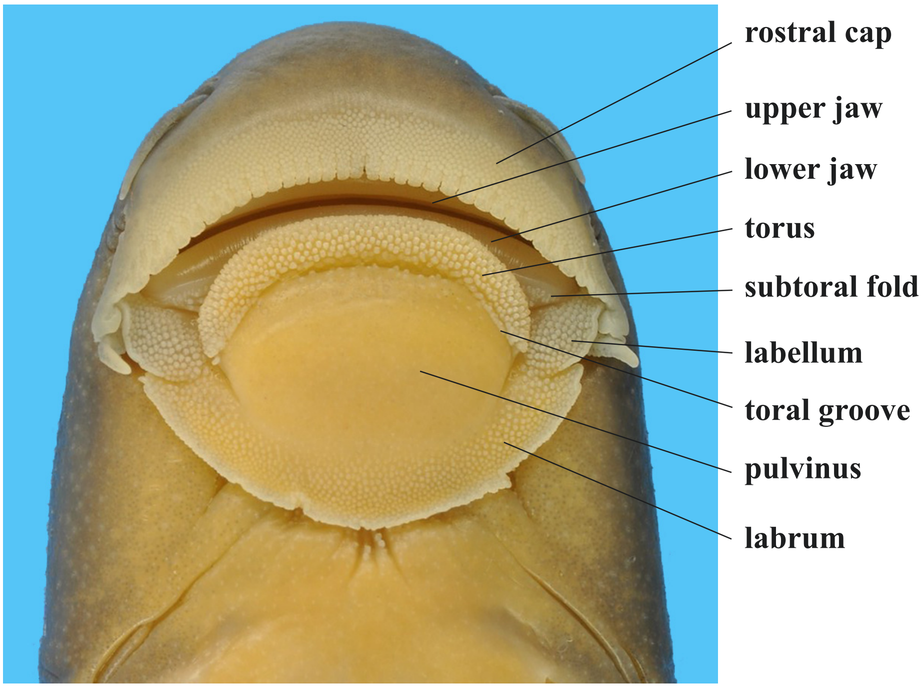

Fig. 3. *Garra dulongensis*, CMK 27239, 104.6 mm SL; ventral view of head, showing external oral and gular morphology.

Fig. 4. Tubercles on head of species of *Ceratogarra*, in lateral and dorsal view. **a,** *C. cambodgiensis*, CMK 23487, 118.3 mm SL; **b,** *C. fasciacauda*, CMK 21999, 93.3 mm SL.

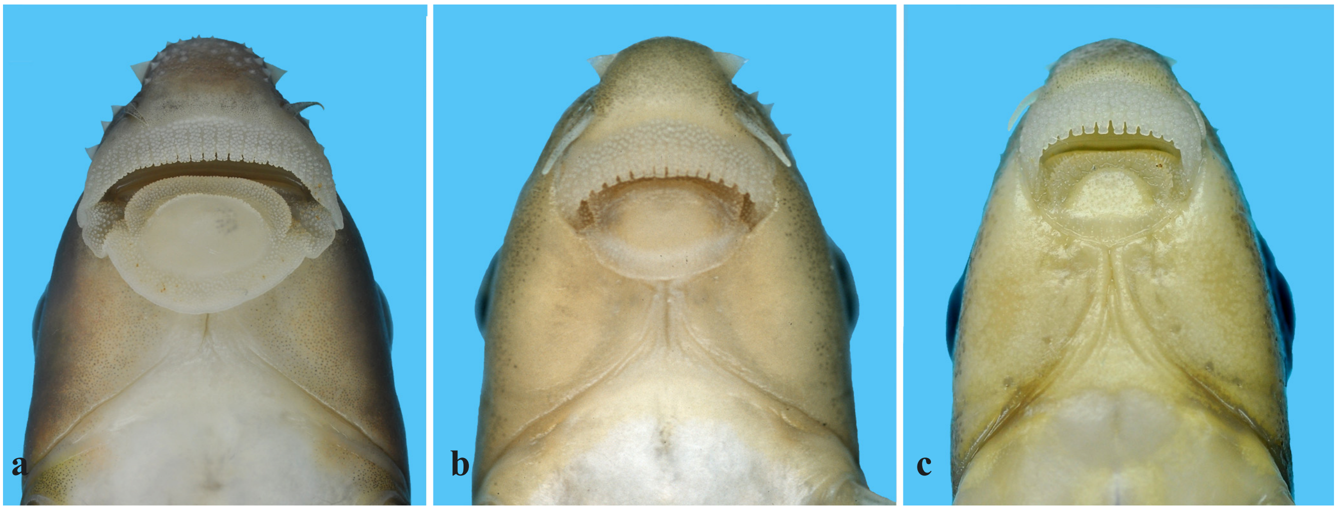

Fig. 5. Mouth and gular disc of *Ceratogarra* species: **a,** *C. cambodgiensis*, CMK 23487, 118.3 mm SL (Xe Kong); **b,** *C. fasciacauda*, CMK 21999, 93.3 mm SL (Xe Kong); **c,** *C. fasciacauda*, CMK 23534, 49.7 mm SL (Nam Ngum).

Fig. 6. *Ceratogarra fasciacauda* (?), CMK 23940, 71.4 mm SL; China: Yunnan: Xishuangbanna: Mekong drainage; possibly *C. bisangularis*.

entirely covered by small papillae; absence of subtoral fold; and absence of proboscis.

Included species. *Ceratogarra cambodgiensis* (Tirant, 1884) is widely distributed on mainland Southeast Asia, in the middle and lower Mekong, Chao Phraya and Mae Khlong drainages, and the northern part of the Malay Peninsula. In the Mekong drainage, it reaches upstream as far as Xishuangbanna (Yunnan, China). There is some intraspecific variation in *C. cambodgiensis* but superficial examination has not yet linked this variation to a geographic pattern.

Ceratogarra fasciacauda (Fowler, 1937) shares the colour pattern and the presence of the large lateral tubercles on the snout of *C. cambodgiensis*; it is missing, however, the yellow colour on the body and the fins; the dorsal fin is hyaline, the caudal fin has black submarginal and white marginal bands and the intermediate area sometimes reddish (Fig. 2). In *C. fasciacauda*, the gular disc is smaller, the labellum and labrum are narrower, and the gular grooves are distinct. *Ceratogarra fasciacauda* occurs even further downriver than *C. cambodgiensis* and has usually been collected over sand to mud bottom; it is less commonly found in rapids in the lowlands. *Ceratogarra fasciacauda* is less common in collections and apparently less abundant. The habitats of *C. cambodgiensis* and *C. fasciacauda* slightly overlap but usually they do not occur in syntopy (I have collected them at the same site only once, out of a total of 220 sites where I observed the genus).

There is some intraspecific variation in *C. fasciacauda* in the shape of the elements of the gular disc and colour pattern. They have not yet been linked to a geographic pattern; research is underway to establish whether this variation indicates the presence of several species. *Garra bisangularis*, described from the Mekong drainage in Xishuangbanna (Yunnan, China), was listed as a possible synonym of *C. fasciacauda* by Kottelat (2013: 104). It is possibly a valid species of *Ceratogarra*, but this cannot be decided from the original description and illustration. The single specimen from Xishuangbanna that I examined has a deeper body than the specimens from central and southern Laos (Fig. 6).

DISCUSSION

Tubercles on snout. Reid (1985: 44–45) described and figured the position of different fields where tubercles are located on the snout in labeonines, and provided a terminology. The diversity of tubercles and their position in *Garra* sensu lato was described and figured by Nebeshwar & Vishwanath (2017), who did not mention Reid's work. They recognised a number of types of organisation of tubercles, but none similar to that observed in *Ceratogarra*. Some species have two prominent tubercles (e.g., *G. birostris*, *G. bispinosa*, *G. arunachalensis*, *G. cornigera*), but in these species the tubercles are at the tip of two lobes of the proboscis, directed forwards and they are acanthoid (multicuspid) (Fig. 7). *Garra mirofrontis* has two conical tubercles, directed laterally, but they are on each side of the tip of the proboscis (on each side of the anterior extremity of the ethmoid field) (Fig. 8).

Fig. 7. *Garra* sp., CMK 22125, 174 mm SL; Thailand: Phangnga.

Fig. 8. *Garra mirofrontis*, CMK 18049, 69.4 mm SL; China: Yunnan: Mekong drainage: Simao.

Some species of *Discogobio* also have a pair of large conical tubercles at the tip of the snout, directed laterally (e.g., *D. tetrabarbatus*; Fig. 9). But in this case, the tubercles are at the very tip of the snout, at each extremity of a transverse lobe, separated from the rest of the snout by a deep furrow. Large tubercles in a similar position as in *Ceratogarra* are also observed in *Paracrossochilus* (see below).

Lower lip, labial fold, disc and terminology. The disc on the ventral face of the head of garras has usually been considered simply as a modified lower lip, without much attention to its details (e.g., Stiassny & Getahun, 2007: 41; Behrens-Chapuis et al., 2015; Hashemzadeh Segherloo et al., 2016). As discussed by Reid (1985: 40) there is no proper lower lip in members of the Labeonini. In cyprinids and especially in most Cyprininae (to which Labeonini belong), the lower lip is made of a thickening of the fleshy covering

Fig. 9. *Discogobio tetrabarbatus*, CMK 21917, 100.4 mm SL; China: Guangxi: Pearl River drainage.

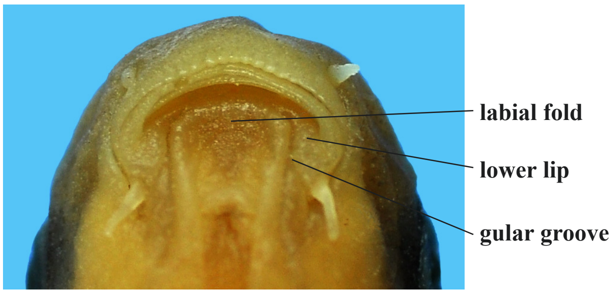

Fig. 10. *Discogobio yunnanensis*, CMK 13079, 25.2 mm SL; juvenile. Note gular grooves and simultaneous presence of lower lip and labial fold.

(corium [dermis and epidermis]) of the edge of the lower jaw. In Labeonini, the corium of the lower jaw is covered by a sheath of keratin; what is usually called lower lip is in fact a skin fold (labial fold) posterior to the edge of the jaw and which, in some genera, may be folded forwards and covers the lower jaw.

Stiassny & Getahun (2007: 47) considered that the "labeonin labial fold is a modification of the lower lip whereby it is separated from the lower jaw by a deep groove" and referred to their figure 6. They seem to have interchangeably used the terms 'lower lip' and 'lower labial fold' (see below) and they apparently considered that the lower lip of cyprinines and the labial fold of labeonines are homologous, whereas Reid (1985) saw both as different structures with different ontogenies. Unfortunately, Stiassny & Getahun were not really explicit and at other places they apparently used 'labial fold' for a groove (e.g., p. 47: "a fold separating the lower lip from the keratinized lower jaw is present to some degree in all labeonins") and their figure 6 is confusing. In their figure 6E (*Labeo*), the 'labial fold' is indicated by an arrow pointing to a groove between the 'lower lip' and the lower jaw, and there is an "upper lip (labial fold)". In their figure 6F (*Garra*) an arrow "labial fold (posterior)" points to a groove between the lower jaw and the "suctorial disc (lower lip)". In their figure 6B (*Labeo*), there is a "lower lip (labial fold)" and an "upper lip (labial fold)" corresponding to what is traditionally called lower and upper lips, and in their figure 6C (*Garra*) there is a "lower lip (labial fold)" label pointing to what seems to be the torus of the gular disc.

The interpretation of Reid (1985) is closer to my own based on the species of Labeonini available to me (all named genera except some of the semilabeonina endemic to China). I distinguish between a lower lip (the thickening of the chorium of the edge of the lower jaw) and the lower labial fold (a fold of skin posterior to the lower jaw [which then is covered by a sheath of keratin]). In some lineages, the fold may be variously thickened, stiffened or ornamented. However, like Hora (1921b), Rauther (1928) and Minzenmay (1933), I consider that a real lower lip may be present in some taxa (at least in young individuals) near the corner of the mouth. That the lower lip and labial fold are different structures is evidenced in taxa in which both are present at the same time (e.g., juvenile *Discogobio*; Fig. 10). The variously shaped and ornamented 'lower lip' of labeonines in fact is not homologous to the lower lip of other cyprinids, and should be called labial fold.

In those labeonine species usually described as 'without lower lip', the labial fold is missing and the tissues of the gular region extend anteriorly about to the edge of the lower jaw (e.g., in *Thynnichthys*; Fig. 11). This is possibly the plesiomorphic condition for Labeonini. In some genera (e.g., *Altigena*, *Labeo*, *Morulius*, *Osteochilus*, *Rohita*; Fig. 12) the labial fold is margined posteriorly by a **plical groove** [plical, adjective: of a fold], more or less developed, strengthening the appearance of the labial fold as a lower lip.

The gular region may be marked laterally by a pair of **gular grooves** (e.g., in *Altigena*, '*Bangana*' *lemassoni*, '*Cirrhinus*' *microlepis*, *Crossocheilus*, *Incisilabeo*, *Mekongina* [Figs. 12c, 13], and juvenile *Discogobio* [Fig. 10]). The gular grooves are possibly an apomorphic feature among Labeonini; they apparently mark the lateral edge of the tissues that develop to make the disc and the other gular structures of various genera. These were called 'mental grooves' by Zheng et al. (2012), which is not appropriate since they are not on the chin but on the gular region. Zheng et al. reported the presence of gular grooves in various taxa/lineages of Labeonini. These gular grooves seem to be homologous with the groove between the torus and the labellum in *Discogobio* (Figs. 9, 10).

Hora (1921b) described and figured the ontogeny of the lips and disc of a species of *Garra* that he identified as *G. rupicola*. In specimens about 20 mm SL, he showed that the disc develops from tissues of the gular region. He identified a lower lip very narrow anteriorly and thicker laterally. He noted (p. 612) that the median part of the lower lip "is replaced by a posterior labial fold" [here, the torus] and that "the thickened portions near the angles separate off and form definite connectives on either side between the upper labial fold [rostral cap] and the posterior border of the disc".

Rauther (1928) studied the morphology and histology of the disc of two species of *Garra* he identified as *G. lamta* and *G. blanfordi*. He interpreted the disc as modification of the integument of the gular region, with its centre under the extremity of the glossohyal (=basihyal in current terminology). He stated that the torus appears first and the pulvinus and labrum appear relatively later. Rauther did not distinguish between lower lip and labial fold, but he always used 'lips' in quotation marks. He commented (p. 67) that 'lips' are distinct in juveniles (without or with rudimentary disc) while in larger individuals they are only distinct at the corner of the mouth and as a row of papillae along the edge of the mouth (apparently the subtoral fold [see below]). [Rauther's ontogenetic conclusions should be read with caution because the observation is based mainly on material of his *G. lamta* from two localities, in which, at the same size, the disc is differently developed. This material is obviously misidentified. *Garra lamta* is a species restricted to northern India. Rauther's material was from "Wadi el Kebir" in "Arabia" and "Ain-et-Tabira on Tiberias Sea" [Tabgha, Israel]. Wadi el Kebir is apparently Nahr al Kabir, at the border between Syria and Lebanon; Rauther's description suggests he had material of a species with a 'reduced' disc, and *G. variabilis* is present in that area (J. Freyhof, personal communication). The species from Tabgha is probably *G. jordanica*, the only *Garra* species known in the Dead Sea and Jordan basin (J. Freyhof, personal communication). Rauther's *G. blanfordi* was from "Adi Naghora, Eritrea"].


Fig. 11. *Thynnichthys thai*, CMK 5114, 140 mm SL.

Minzenmay (1933) studied the morphology of the mouth of numerous species of Cyprinidae. He did not make a distinction between the lower lip and the labial fold. But he described the situation in numerous species in which the lower lip is restricted to the corner of the mouth and he labelled the whole intermediate area "Kehlregion" or "Kehlbezirk" [throat area, gular area; in German], which he defined as the "area delimitated by the branchiostegal rays and the lower lip". Minzenmay (1933: 223) misunderstood Hora's 'connectives' as connecting the "lower labial fold" [instead of upper, that is rostral cap] and the posterior border of the disc.

The distinction between lower lip and labial fold requires adjustment to the terminologies in current use. The disc has been referred to as labial disc or mental disc. Since it is not derived from the lower lip, as shown by Hora (1921b), Rauther (1928) and Minzenmay (1933), it is incorrect to call it 'labial disc'. Neither is it appropriate to call it 'mental disc' since it is well behind the chin (the central forward part of the lower jaw). Since it seems to be entirely formed by tissues of the gular region, it is more appropriately called the **gular disc**. The adjectives 'suctorial' or 'adhesive' have often been used in descriptions. Since the disc can be identified unambiguously without mention of a function, these adjectives are not needed. Furthermore, it is not demonstrated that the disc is 'suctorial' or 'adhesive' in all species; in fact, in a number of species the disc is either very poorly developed or reduced and it is unlikely to have any suctorial or adhesive abilities.

The terminology in present use for the elements of the disc has been proposed by Zhang et al. (2002: 209; Zhang & Zhou, 2012: 18). It has been adopted by some authors including Stiassny & Getahun (2007) and Nebeshwar & Vishwanath (2013, 2017) while other authors have used slightly

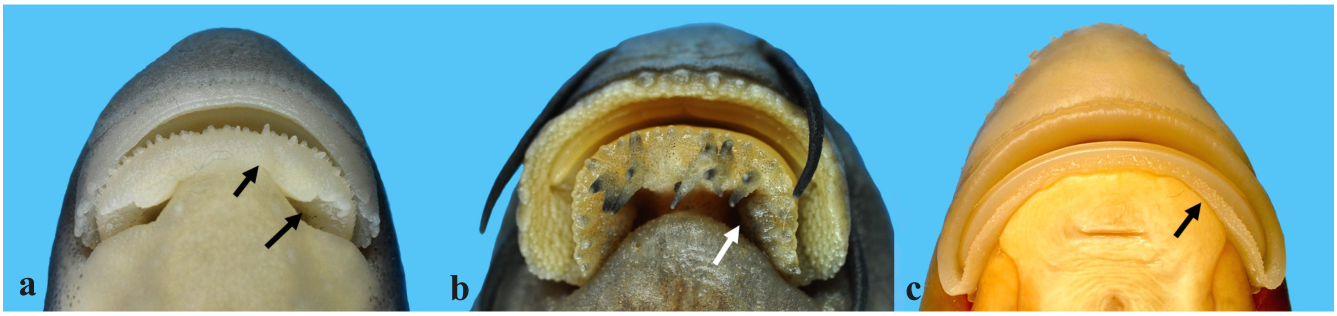

Fig. 12. Plical groove (arrows) in: **a,** *Labeo pierrei*, CMK 23536, 99.3 mm SL; **b,** *Morulius chrysophekadion*, CMK 13387, 104.6 mm SL; and **c,** *Altigena lippa*, CMK 22415, 137 mm SL.

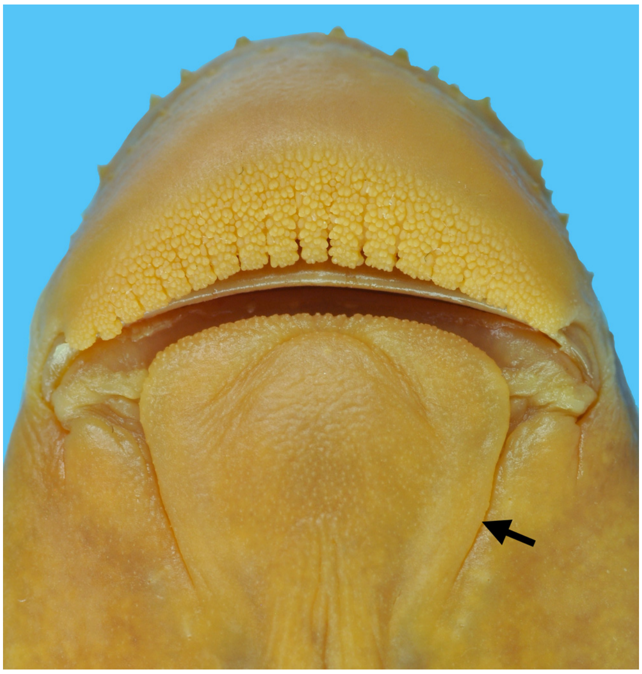

Fig. 13. *Mekongina erythrospila*, CMK 13816, 138 mm SL. Arrow points to gular groove.

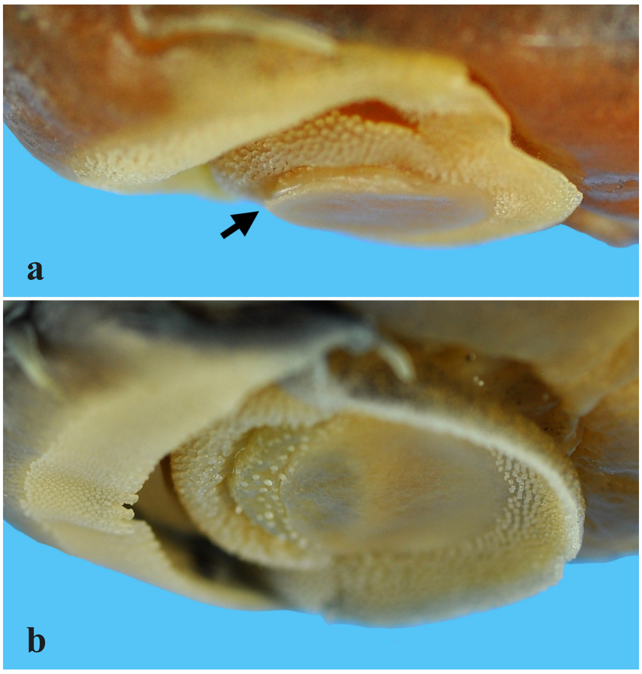

Fig. 14. Respective positions of the pulvinus and torus in: **a,** *Ceratogarra cambodgiensis*, CMK 5189, 81.7 mm SL, with the pulvinus (arrow) extending over the posterior part of the torus; and **b,** *Garra bourreti*, CMK 25786, 96.5 mm SL, with the pulvinus behind the torus.

different terms (e.g., Kullander & Fang, 2004: 258). I found Zhang et al. (2002) terminology cumbersome because it uses unnecessary long compound words and in several instances the words are misleading since they are not used with their correct meanings. I use here a revised and straightforward terminology (see also Fig. 3).

Zhang et al. (2002) called 'central callous pad' the "fleshy pad of thickened skin on the central portion of the mental adhesive disc, anteriorly separated from the anteromedian fold by a transverse groove". This element was called 'central pad' by Kullander & Fang (2004), and defined as "smooth or little papillose central portion of the lower lip, margined anteriorly and posteriorly by bands of papillae". I do not think that 'callous' should be part of the name of the element, because the adjective adds no information and also this central pad is not callous (having calluses; toughened), or at least not in all species. The important point to note here is the position, and central pad of the gular disc would seem descriptive enough and unambiguous. The presence or absence of papillae is not relevant to the definition; the central pad is partly papillose in *Ageneiogarra*, *Discogobio* (Fig. 9) and probably other genera. To facilitate discussion, instead of a compound word, I refer to this central pad as **pulvinus** (plural pulvini), from the Latin word meaning pillow. The word has already been used in the formation of the names *G. propulvinus* (see Kullander & Fang, 2004) and '*Ageneiogarra*' *micropulvinus* (see Zhou et al., 2005).

The anterior element of the disc was called 'anteromedian fold' by Zhang et al. (2002: 209). They defined it as "a fleshy flap of skin which is formed by the anterior border of the mental adhesive disc, posterior to the horny sheath on the lower jaw and anterior to the central callous pad". Kullander & Fang (2004) called it a band of papillae. 'Anteromedian' seems redundant, since an element in front of a central element is median, by definition. In the species that I have examined, it is not a real fold and it is in no case a flap. It is a swollen transverse mass, more or less round in cross section, densely covered by papillae, separated from the pulvinus by a groove and its anterior margin is free. This corresponds to the observations of Minzenmay (1933: 225) who called it "vordere Querwulst" [anterior transverse fold; in German] or "vordere Wulst der Haftscheibe" [anterior fold

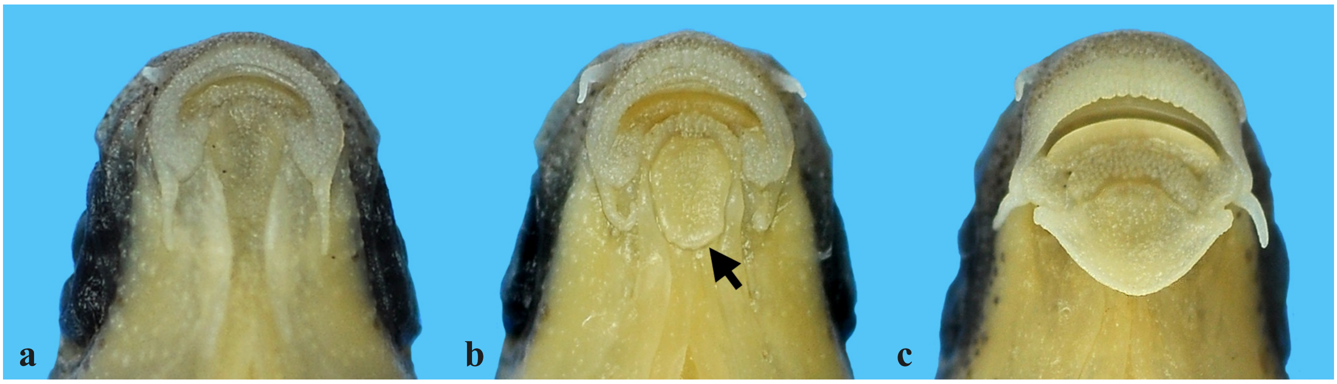

Fig. 15. *Garra* sp., CMK 15198; Thailand Mae Khlong drainage; labrum formed from tissues of center of gular area; **a,** 13.8 mm SL; **b,** 15.2 mm SL; **c,** 20.4 mm SL. Arrow indicates shallow groove posterior to pulvinus.

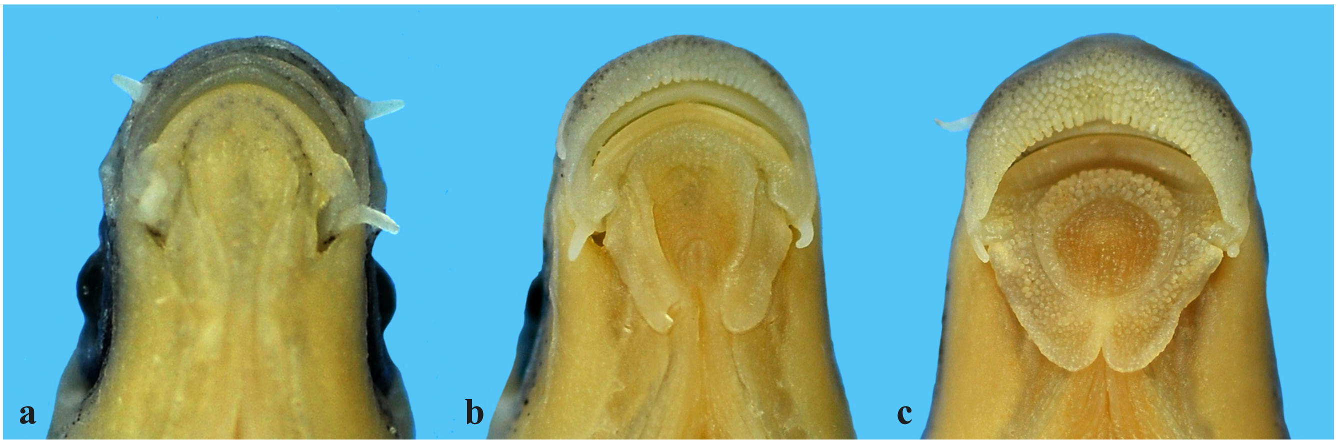

Fig. 16. *Ageneiogarra theunensis*, CMK 22573; labrum formed by median fusion of tissues from sides of gular area; **a,** 18.6 mm SL; **b,** 22.4 mm SL; **c,** 27.3 mm SL.

of the adhesive plate]. Minzenmay identified the ontogeny of the 'vordere Querwulst' as a transverse fold of the gular area that precedes the formation of the pulvinus. I call it **torus** (plural tori), from the Latin word meaning a roll of flesh; the word describes the structure and position, and adjectives will be necessary only to describe its shape. It seems that the torus is derived from (or homologous to) the labial fold, but this remains to be demonstrated by developmental series. The groove between the torus and the pulvinus does not seem to be homologous to the plical groove and I call it **toral groove** (Fig. 3). In most garras, it appears as if the torus is rolled backwards over the anterior edge of the pulvinus and forms the groove; in *Ceratogarra*, it seems that the pulvinus is pushed forwards above the posterior edge of the torus (Fig. 14), and the groove may have a different ontogeny.

In *Ageneiogarra*, the anterior edge of the torus appears as a thin fold, against the jaw. This fold seems to be part of the torus (with which it is continuous) and does not seem to be homologous to the subtoral fold (see below).

Zhang et al. (2002: 209) recognised a 'lateroposterior flap' that they defined as "a free, loose, membranous, peripheral flap of skin surrounding lateral and posterior portion of the central callous pad, superficially covered with numerous papillae". I do not think that 'flap' (defined as a movable piece of material attached at one edge and usually covering an opening) is the appropriate word to describe this element. It is more appropriately called 'flange' (a wide edge on a pillow etc., extending from the outer seam). Lateroposterior is unnecessarily complex, it is enough to say it is posterior (it margins the whole posterior half of the central pad). Posterior flange would have been descriptive enough and since there is only one flange, it could be enough to say flange, although the addition of posterior may make it easier to remember its position. I call it **labrum** (plural labra), the Latin word meaning flange, a projecting edge; or the wide edge of a pillow.

Zhang et al. (2002: 209) distinguished an 'anterolateral lobe' that they defined as "a fleshy lobe of skin with discrete margins, lateral to the end of the anteromedian fold and bridging the rostral fold and lateroposterior flap of the mental adhesive disc around the corner of the mouth". The correct meaning of lobe is: rounded projection forming part of an organ; or a subdivision of a bodily organ or part, delineated by shape or connective tissue (Collins English Dictionary; https://www.thefreedictionary.com/lobe). Minzenmay (1933: 225) identified the lateral lobe as "Mundwinkelwulst" [fold at corner of mouth, or thickening at corner of mouth], which he considered to be the remnants of the lower lip (p. 224), connected to the labrum by a "Konnectiv". Hora (1921b: 642) had identified as "connective" the remnants of the lower lip itself. The 'anterolateral lobe' appears on figures 1C and 6C of Stiassny & Getahun (2007: 51), but it is labelled as "rostral frenum (continuous with lower lip)" on their figure 8 showing *Discocheilus*, *Discogobio*, *Placocheilus* and other Labeonini. However, on their figures 1C and 6C, the rostral frenum is not mentioned, but there is a "frenum of rostral cap (continuous with lower lip)". I accept the 'anterodorsal lobe' as modified lower lip and call it **labellum** (plural labella), from the Latin word meaning small lip, alluding to the small size of this remnant of the lower lip.

In some species, a small papilliferous fold extends mediad from each corner of the mouth, posterior to the lower jaw and under the torus; in some species this fold is continuous and in some it is interrupted. Kullander & Fang (2004) called this structure "pleated papilliferous fold" (singular), followed by Nebeshwar & Vishwanath (2017: 28), who treated it as two folds (one on each side) sometimes connected medially by a "membranous flap". This papilliferous fold is here called **subtoral fold** (Fig. 3). Rauther (1928: 67) apparently interpreted the subtoral fold as remnants of the lower lip. The subtoral fold might in fact be the labial fold.

In some species of garras, the labella are missing or cannot be distinguished from the labrum (at least on published figures). In figures of other species, it seems that the labrum in fact could be the two labella meeting medially behind the pulvinus. For example, the figures of *Garra incisorbis* in the original description (Zheng et al., 2016: fig. 2a) and in Gan et al. (2017: 207) show a soft and papillated pulvinus (?), with a posterior groove interrupted medially and the labrum (?) with a median posterior notch.

In fact, the labrum in different lineages has a different ontogeny and is not homologous. In *Garra* sensu stricto, the pulvinus forms as a thickening in the gular area and a fold develops backwards that becomes the labrum (Fig. 15). In *Ageneiogarra*, the labrum develops as a pair of folds along the gular grooves (on the external side) that meet medially to encircle the gular area, which develops as a pulvinus (Fig. 16). This corresponds to the situation observed in adults of '*A*'. *incisorbis*, '*A*'. *micropulvinus*, *Sinigarra* and maybe *Vinagarra* (see below), *Hongshuia paoli* (figured in Gan et al., 2017: 205). This also explains the different shape of the torus (see below). A further discussion of the ontogeny of the gular disc is beyond the scope of the present article.

In all species of disc-bearing garras that I examined (see Comparison material), the pulvinus and the torus of the gular disc are clearly demarcated and do not overlap. In *Ceratogarra*, the mouth and the pulvinus are smaller than in the other disc-bearing garras in South, Southeast and East Asia (width of pulvinus about 2–3 times in the width of the head at the same location, vs. about 1.5–2). In *Garra*, the pulvinus is fleshy, cushion-like, and the torus is present since the earliest stages of development available for study (about 15 mm SL) and appears as if 'rolled' backward in the groove between it and the pulvinus (Fig. 14b). In *Ceratogarra*, the pulvinus is flatter and thinner and expands forward as a short blade that covers the posterior edge of the torus (Fig. 14a). In the smallest available specimens of *C. cambodgiensis* (CMK 8188, 28.6 mm SL; CMK 10736, 3, 28.3–31.0 mm SL) the disc is completely formed, the pulvinus is thick and overlaps the torus, and the torus is narrow. [Despite the large number of samples of *C. cambodgiensis* and the number of field sites where it was obtained in Laos, no smaller specimen has ever been seen. Since all sampling had been done between December and June, this suggests that spawning occurs between July and October].

In *Ceratogarra*, the posterior edge of the pulvinus is not as well set apart from the labrum as in *Garra* and *Ageneiogarra*. This is especially the case in some individuals of *C. fasciacauda* in which the pulvinus is much reduced (Fig. 5c). Juveniles are needed to see whether the pulvinus, torus and labrum of *Ceratogarra* are homologous (have the same structure and ontogeny) with those of *Garra* sensu stricto.

Lineages of garras. *Garra* sensu lato had long been suspected or hypothesised to be polyphyletic (personal observation and, e.g., Zhou et al., 2005) but this has been neither investigated in detail at the global level nor formalised in the nomenclature. After a global (but much outdated) revision by Menon (1964), research on garras has been geographically restricted. The oral morphology and tuberculation pattern of most South, Southeast and East Asian species have been reviewed by Nebeshwar & Vishwanath (2017). Chinese species have been reviewed by Zhang et al. (2000); several additional species have been described since. Stiassny & Getahun (2007) revised the African species but did not address the Asian species. Krupp (1983), Hamidan et al. (2014), Sayyadzadeh et al. (2015), Esmaeili et al. (2016), Lyon et al. (2016), Freyhof (2016) and others studied the species from Southwest Asia.

Various molecular studies included a number of species of garras but again they were geographically limited (e.g., Zheng et al., 2012; Geiger et al., 2014; Hamidan et al., 2014; Behrens-Chapuis et al., 2015; Hashemzadeh Segherloo et al., 2016) and included too small a number of species to reach taxonomic conclusions on the whole genus. Yang et al. (2012) included 29 species of *Garra* sensu lato (including the type species *G. lamta*) in a study of the whole tribe Labeonini; their coverage for Southwest Asia and Africa, however, remained limited; the identity of their material of *G. lamta* needs confirmation. Geiger et al. (2014), Hamidan et al. (2014) and Hashemzadeh Segherloo et al. (2016) focused on Southwest Asian and African species; they analysed 26 of them and included 14 species from other areas from earlier studies.

Yang et al.'s (2012) analysis included *C. cambodgiensis* and *C. fasciacauda* and showed that they are not closely related to other garras and, as expected, that they are sister species. Their analysis also showed that *Garra* as commonly understood is not monophyletic, that is, the gular disc is present in several lineages of Labeonini in the subtribes Garrina and 'semilabeonina' but in both subtribes there are lineages without disc. Zheng et al. (2010, 2012) recovered the same general pattern in a similar study of Labeonini, but with a smaller

Fig. 17. *Ageneiogarra theunensis*, CMK 22502; Laos: Nam Ngum watershed. **a, c,** 154 mm SL; **b,** juvenile, 36.4 mm SL. Yellow arrows: lateral extension of torus; black arrow: anterior fold of torus.

taxonomic and geographical coverage. Some of their sequences were included in the study of Yang et al. (2012).

Yang et al. (2012) found that *G. imberba* and *G. micropulvinus* belong to a distinct lineage, outside the subtribe Garrina but in a subclade of their subtribe 'semilabeonina', which also included some of the East Asian '*Bangana*' sensu lato, *Altigena* and *Mekongina*, all without disc (see Kottelat, 2017). They retained this garra lineage as a distinct genus, *Ageneiogarra*. As observed in the present study, species of *Ageneiogarra* (Fig. 17) are distinguished from *Garra* sensu stricto, among others, by the different ontogeny of the gular disc, especially that of the labrum (see above). This results in having the torus separated from the pulvinus by a deep groove and extending laterally and posteriorly along the sides of the pulvinus as a narrow strip of tissues, separated from the labrum by a deep groove (Fig. 17a,b). Other characters that diagnose *Ageneiogarra* are: the anterior edge of the torus appears as a thin fold, against the jaw, crenulated at least laterally [not alway distinct; absence seems to be an artefact of preservation]; a band of small papillae extending from the posterior edge of the pulvinus towards the center (as in *Discogobio*, but less distinct); tiny tubercles on snout; large adult size (up to at least 300 mm SL); no barbels in adults; about 46–50 total lateral line scales; and the anus is closely behind the pelvic-fin base. In the other garras, the anus is halfway between pelvic-fin base and anal-fin origin (or behind); the torus does not extend laterally between the pulvinus and the labrum; the torus lacks a narrow anterior fold against the lower jaw; and there is space between the torus and the lower jaw. '*Ageneiogarra*' *micropulvinus* does not agree in all characters with *Ageneiogarra* and is only tentatively referred to this genus.

In addition to *Ageneiogarra*, the 'semilabeonina' of Yang et al. (2012) include three additional genera with gular disc, *Discogobio*, *Discocheilus* and *Placocheilus* (whose validity has been debated; see below). In Yang et al.'s (2012) analysis, these genera belong to distinct lineages, each also including genera without gular disc. Although the disc of adult *Discogobio* may appear homologous to that of *Garra*, the situation in the juvenile of *Discogobio* is quite distinct. In two juveniles of *D. yunnanensis* (CMK 13079, 25.2 mm SL; CMK 13091, 25.4 mm SL), the lower lip is still clearly distinct near the corner of the mouth, the labial fold ends anteriorly at the edge of the lower jaw and is marked laterally by gular grooves, leaving a squarish median area on which no specific structure can be distinguished (Fig. 10). A small pit and skin fold, if not a fixation artefact, suggest a possible future position of the labrum. The shape of the labial fold is

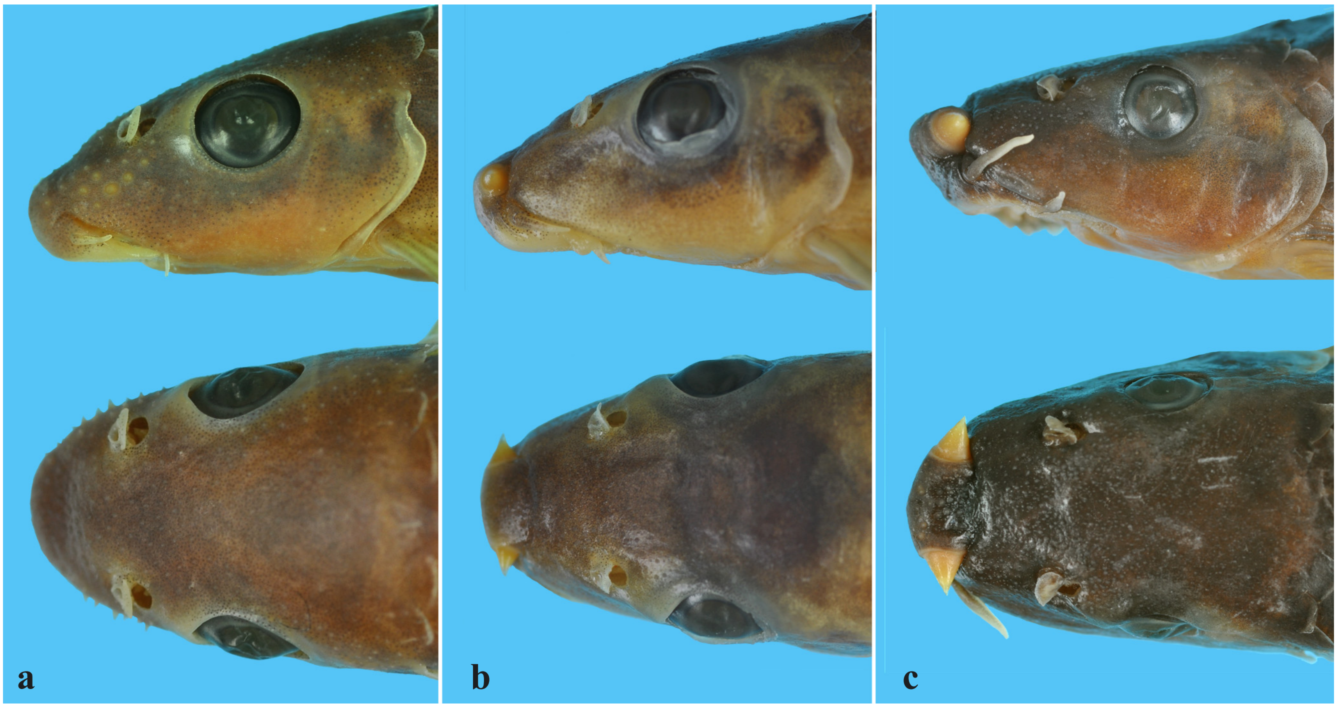

Fig. 18. Tubercles on head of *Paracrossochilus* species: **a,** *P. acerus*, CMK 10590, 42.8 mm SL; Borneo: Kapuas drainage; **b,** *P. vittatus*, CMK 11527, 49.0 mm SL; Borneo: Kapuas drainage; **c,** *P. vittatus*, CMK 10831, 63.9 mm SL; Borneo: Sarawak.

similar to that observed in *Mekongina* (Fig. 13), also a member of the clade 'semilabeonina', but which never develops a disc. In the adult *Discogobio*, the torus (or its analogue) is greatly arched and surrounds three sides of the pulvinus (or its analogue). The centre and posterior part of the pulvinus of *D. tetrabarbatus* are covered by a band of harder tissue supporting papillae and expanding forwards from the labrum (or its analogue) (Fig. 9). There is no apparent discontinuity between the labella and the labrum. It seems that the disc of *Discogobio* is not homologous with that of *Garra* and shares features in its ontogeny with *Ageneiogarra*.

The subtribe 'semilabeonina' is the sister group to the 'osteochilina', which does not include any species with gular disc. The lineage 'semilabeonina' + 'osteochilina' is the sister group to Garrina. Yang et al. (2012) recovered the bulk of garra species in the subtribe Garrina. Most of them belong to a monophyletic lineage (*Garra*), which is the sister group to a lineage including *Tariqilabeo* and *Akrokolioplax.* Based on the assumption that all sequenced species have been correctly identified, even within such a concept of *Garra*, some lineages can be recognised, which correspond to morphologically distinctive groups of species, for example: species with a deep body, patterned caudal fin, rostral barbels inserted on the lips (vs. in a groove) and a thin torus with free, rounded lateral extremities (*G. flavatra* and *G. lissorhynchus*); species with a long projecting proboscis (*G. fuliginosa*, *G. orientalis*, *G. mirofontis* and *G. cyrano*).

Yang et al. (2012) recovered *Ceratogarra cambodgiensis* and *C. fasciacauda* as a lineage sister to *Paracrossochilus vittatus*, all three together the sister group to all other Garrina (see below).

At least two other genera of garras with gular disc have been named, *Sinigarra* and *Vinagarra* from southern China and Vietnam. Their close relationships with any of the garra lineages remain to be confirmed. As described and figured by Zhang & Zhou (2012), the gular disc of *Sinigarra* has no torus, the posterior edge of the pulvinus is separared from the labrum except medially, and the labrum has a median incision reaching forward until the posterior edge of the pulvinus. The mouth parts appear fleshy, and there are no tubercles. The figures of *S. napoensis* in Gan et al. (2017: 206) do not allow to recognise a pulvinus and a labrum. A recently published study by Yao et al. (2018) places *S. napoensis* as sister species to *Altigena*; *Ageneiogarra* and '*A*'. *micropulvinus* were not included in this part of the study. The number of species included in Yao et al.'s study is smaller than in Yang et al. (2012) but many sequences are the same and this suggests that Yao et al.'s (2018) *Sinigarra* + *Altigena* clade is the same clade as that including *Ageneiogarra*, '*A*'. *micropulvinus* and *Placocheilus* in Yang et al. (2012). The median incision of the labrum in *Sinigarra* also suggests affinities with *Ageneiogarra*.

Vinagarra has not yet been included in any molecular analysis. As described and figured by Li et al. (2008) for *V. findolabium*, the gular disc of *Vinagarra* has a torus very arched, extending laterally along the pulvinus (without groove separating them), with strong papillae; the pulvinus does not have a distinct posterior edge; the labrum is divided by a notch extending forward until, and sometimes continued into, the pulvinus; and there are no labella. The English abstract and the figures of the original description of *Vinagarra* (Nguyen & Bui, 2009), and the comments and pictures of the three Vietnamese species of *Vinagarra* by Endruweit (2014) do not provide additional information.

Fig. 19. *Paracrossochilus vittatus*, CMK 11527, 49.0 mm SL; Borneo: Kapuas drainage: Danau Sentarum.

Fig. 20. *Paracrossochilus acerus*, CMK 21824, 60.6 mm SL; Borneo: Mahakam drainage: Belayan watershed.

Again, the median notch of the labrum suggests affinities with *Ageneiogarra*.

The trees in Yang et al. (2012) and Zheng et al. (2012), with mainly South and East Asian species included, and those of Hashemzadeh Segherloo et al. (2016) and Behrens-Chapuis (2015), with mainly Southwest Asian species, have only a few species in common. However, the Southwest Asian COI trees show a clade of a few species (including *G. variabilis* and *G. mullya*) sister-group to all other *Garra* (except *G. kempi* from Northeasten India, *G. bicornuta* from Peninsular India, *G. flavatra* from Myanmar, and *G. tengchongensis* from the Irrawaddy drainage in China). In the tree of Yang et al. (2012) this *G. variabilis*–*G. mullya* clade is also sister to a clade that includes all the sequenced African and Southwest Asian species, and *Phreatichthys*, *G. lamta* (type species of *Garra*), *G. gotyla* and the *G. orientalis* clade. In this tree, *G. flavatra*, *G. tengchongensis* and *G. kempi* are in three lineages outside the two main lineages, and *G. bicornuta* is in the *G. variabilis* clade. Preliminary observations suggest that there apparently are characters usable to define all these lineages, but this still requires more work and decent material of more species. Zheng et al. (2012) included fewer species, and none from Southwest Asia and thus no comparison is possible. They included *G. tengchongensis*, which again has a separate position, as sister-group to *Tariqilabeo* + *Akrokolioplax*.

Paracrossochilus. The large tubercles and their position in *Ceratogarra* are also observed in *Paracrossochilus* (Fig. 18), the sister group recovered by Yang et al.'s (2012) molecular analysis. The genus *Paracrossochilus* is endemic to Borneo. Two valid species of *Paracrossochilus* are presently recognised (*P. vittatus*, Fig. 19; *P. acerus*, Fig. 20); the examined material suggests that more species await description (personal observation). The two species of *Paracrossochilus* also share the colour pattern made of a broad, contrasted dark brown to black midlateral stripe on a pale brown background and whitish to yellow lower half of flank; the submarginal bands along the upper and lower edges of the caudal fin are also present, but fainter. *Ceratogarra* is distinguished from *Paracrossochilus vittatus* (the type species of the genus) by the presence of the gular disc (vs. absence).

Weber & de Beaufort (1916: 226) described the 'lower lip' of *Paracrossochilus vittatus* as forming "a median prominent broad body, emarginated anteriorly, rounded laterally, not separated from the isthmus [...]. It has on each side a lateral part, forming a soft, curved prolongation connected with the upper lip, situated in a deep groove representing the lateral part of a postlabial groove, where it is folded". The 'median part of the lower lip' is the labial fold. It is fleshy and very thick (about as thick as wide), not adnate to the lower jaw, densely papillated, also along the anterior edge; the anterior edge is deeply notched in the middle, with a shallow depression behind each half; there is a fleshy pad (gular pad) on the gular region behind the labial fold (Fig. 21). In the largest specimen available (63.9 mm SL; Fig. 21b), the depressions become deeper, the gular pad becomes less prominent but seems connected to the middle of the labial fold by a frenum, which is responsible for pulling backwards the median part of the labial fold, forming the notch and the two depressions. On each side, 'the lateral parts of the lower lip' apparently are remnants of the lower lip. Each appears as a wide flange, relatively thin, densely papillated, connected to the rostral cap (Fig. 21a).

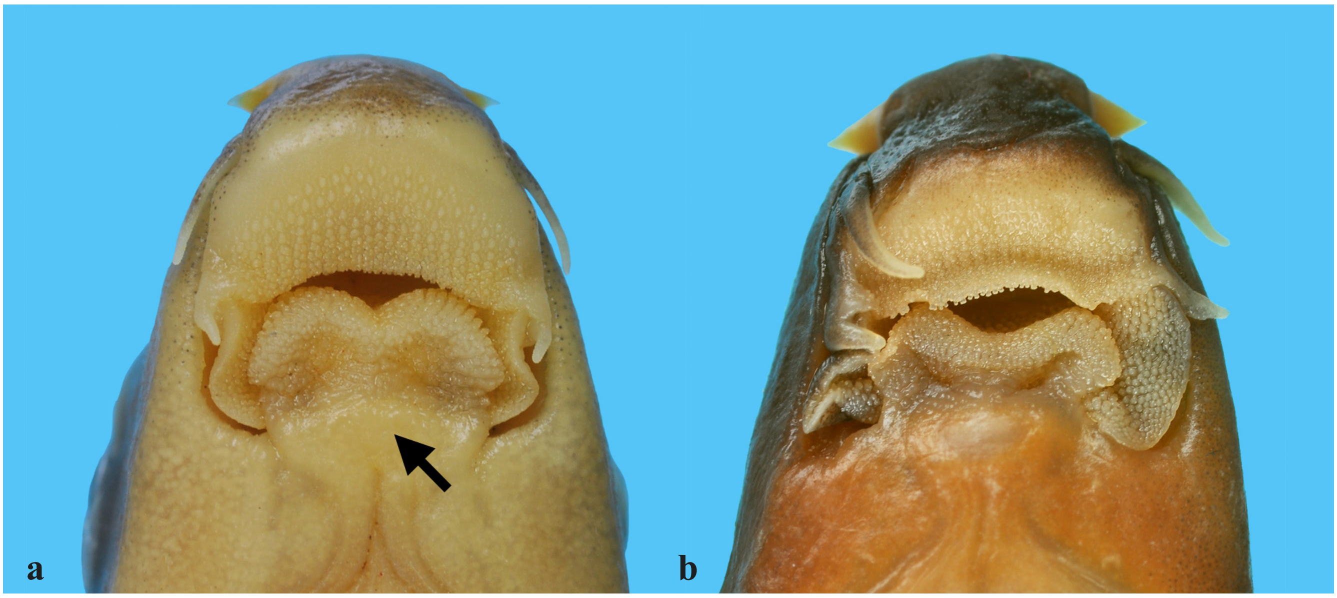

Fig. 21. *Paracrossochilus vittatus*, mouth; **a,** CMK 11527, 49.0 mm SL; Borneo: Kapuas drainage; **b,** CMK 10831, 63.9 mm SL; Borneo: Sarawak. Arrow: gular pad.

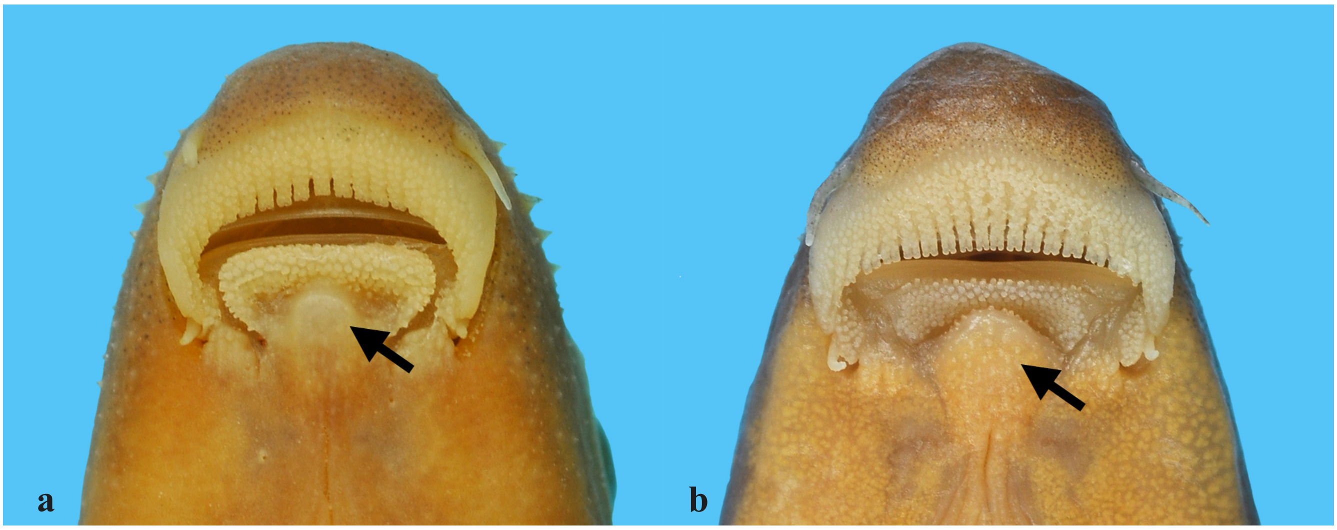

Fig. 22. *Paracrossochilus acerus*, mouth; **a,** CMK 10590, 42.8 mm SL; Borneo: Kapuas drainage; **b,** CMK 10848, 55.5 mm SL; Borneo: Kapuas. Arrows: gular knob.

Paracrossochilus acerus has a great overall similarity with *P. vittatus*, but differs by the presence of only small tubercles (Inger & Chin, 1962; Fig. 18a). The morphology of the lower lip and labial fold is somewhat different (Fig. 22). The labial fold is thinner, not notched anteriorly, it does not form two depressions, and the gular pad forms a fleshy triangular knob (gular knob), pointed forwards and covering part of the middle of the labial fold, leaving a groove between them. The gular knob seems to correspond to the position of the basihyal. The anterior edge of the gular knob is papillated. The remnants of the lower lip are almost completely hidden in the postlabial groove. In specimens about 23 mm SL, the gular knob is already visible, outlined by a shallow groove behind the labial fold. In specimens about 40–50 mm SL, the knob seems connected to the labial fold by a frenum. This frenum is thicker and less obvious in larger specimens (up to 78.8 mm SL; ZRC 46777).

Comparing the oral and gular structures of *C. fasciacauda* and *P. acerus*, it is tempting to see a homology between the pulvinus in *C. fasciacauda* and the gular knob in *P. acerus*, and between the torus of the former and the labial fold of the latter species. Again, these homologies should be reevaluated carefully when small juveniles of all species become available.

Zoogeography. *Ceratogarra* and *Paracrossochilus* have a disjunct range, with *Ceratogarra* endemic to the Indochinese area and *Paracrossochilus* on Borneo; there are no related genera or species on Sumatra and Java. This distribution pattern is shared with a number of other pairs of taxa or lineages: Gyrinocheilidae (two Indochinese and one Bornean species), Gastromyzontidae (Crossostomatinae on the mainland and Gastromyzontinae on Borneo), *Pterocryptis* (all species on mainland and *P. furnessi* on Borneo). *Garra borneensis* and *G. robertsi* are known from Borneo; this genus too is missing on Java and Sumatra. It is noteworthy

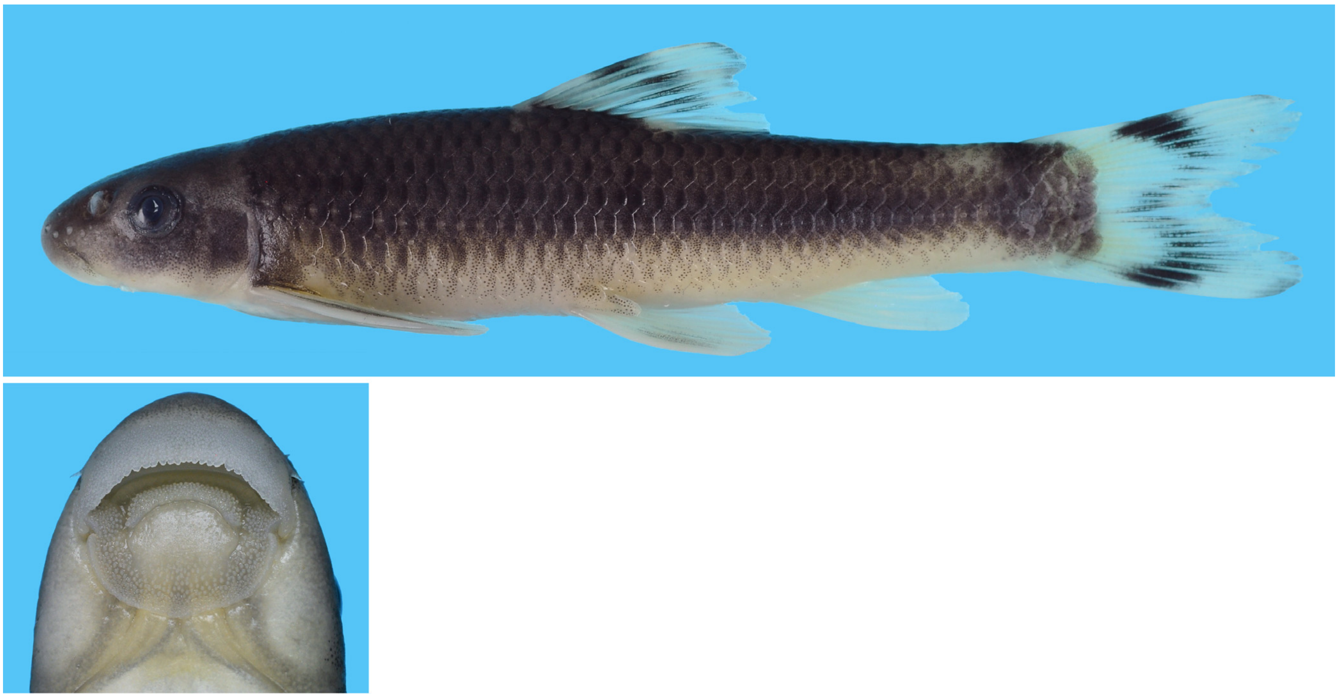

Fig. 23. *Placocheilus caudofasciatus*, CMK 25745, 47.3 mm SL; Laos: Nam Ma drainage.

that these lineages are made of species with rheophilic morphological features, inhabiting fast flowing habitats in hilly areas. Virtually all lowland species or genera shared by Borneo and the mainland also occur in Sumatra and Java, and their distribution and relationships reflect the interconnections of these areas when the Sunda Shelf between them was exposed several times and allowed movement between the islands and the mainland (Molengraaff & Weber, 1919; Beaufort, 1951; Brittan, 1954; Kottelat, 1989; Rainboth, 1991; Voris, 2000; Sathiamurthy & Voris, 2006). The movement across the lowlands was more difficult for rheophilic species, and it seems a reasonable hypothesis that their isolation predated or occurred in the earliest glacial episode(s).

Assuming a topography similar to the present, a connection of rheophilic habitats between Sumatra and the mainland would more easily happen on a road through the Malay Peninsula than on a road across the Mekong/PaleoMekong/Chao Phraya and through Borneo. Indeed, the rheophilic fauna of Sumatra shares a few species with the Malay Peninsula that are missing on Borneo (several *Glyptothorax* species [Ng & Kottelat, 2016]) and also has its own endemic genus, *Homalopterula* (Kottelat, 2012, 2013).

Two named species of *Garra* sensu lato are known from Borneo, *G. borneensis* and *G. robertsi*. They have not yet been included in any molecular analysis. Their relationships with the mainland *Garra* are not yet established. Interestingly, in these two species the pulvinus of the gular disc is lamellar and the anterior edge is thin and covers the posterior edge of the torus, as in *Ceratogarra* (or as the gular knob and labial fold in *Paracrossochilus acerus*). This is observed in individuals of the size range 15–135 mm SL. Future studies should check whether they are possibly more closely related to *Ceratogarra* and *Paracrossochilus* than to the other mainland garras.

Placocheilus. *Placocheilus* has been treated as a synonym of *Garra* by some authors (Zhou et al., 2005) and as a valid genus by others (Zhang, 2005; Zhang et al., 2002; Chen et al., 2012; Zhou et al., 2015). Yang et al.'s (2012) results should have settled this issue as they established the distinctness of *Placocheilus*, if it were not that they only included *P. cryptonemus* but not the type species (*P. caudofasciatus*; Fig. 23). In fact, *Placocheilus* itself is an artificial genus. *Placocheilus* as currently understood (e.g., Chen et al., 2012) includes four or five species; two (or three depending of authors) of them (including *P. caudofasciatus*) are known from the Red River drainage, *P. cryptonemus* from the Salween drainage, and *P. dulongensis* from the upper Irrawaddy drainage. This disjunct distribution is otherwise unknown in Southeast Asian fish genera and immediately calls for a more critical evaluation.

Placocheilus caudofasciatus and *P. cryptonemus* have quite distinctive appearances that do not suggest close relationships. Indeed, a later analysis by Wang et al. (2014: 29) placed *P. caudofasciatus* and *P. cryptonemus* in 'semilabeonina' close to, but outside of, *Ageneiogarra*, and both did not form a monophyletic lineage, which suggests that they probably belong to distinct genera (in which case the genus including *P. cryptonemus* is apparently unnamed). The two species also differ in mouth shape (see figures in Chen et al., 2012). The placement of *P. dulongensis* (Fig. 24) in *Placocheilus* instead of *Garra* relies mainly on the presence of only two rows of pharyngeal teeth instead of three. This kind of reductive character, alone, is not sufficient to diagnose *Placocheilus* as monophyletic but rather could have evolved in parallel in several lineages of garras. The materi-

Fig. 24. *Garra dulongensis*, CMK 27272, 97.5 mm SL; Myanmar: Irrawaddy drainage: Mali Hka.

al I identify as *P. dulongensis* belongs to *Garra*. A recent molecular study (Gong et al., 2018a) retrieved *G. dulongensis* within *Garra*, in a clade including *G. dengba*, *G. tengchongensis* and a *G.* cf. *kempi* (apparently *G. tibetana* Gong et al., 2018b).

Parapsilorhynchus. *Parapsilorhynchus* was first listed as a synonym of *Garra* by Roberts (1989: 40). The genus is recorded only from Peninsular India. It was created by Hora (1921a) for *P. tentaculatus* and *P. discophorus*. Hora used as diagnostic characters for the genus, among others, "the lower lip is very prominent, and usually there is either an indication of or a rudimentary disc behind it". Later, Hora (1926: 457) treated *P. discophorus* as a synonym of *P. tentaculatus*, a decision not followed by Yazdani & Singh (1991). Hora & Misra (1938: 32) described *P. prateri* and Singh (1994) described *P. elongatus*. A fifth species, *P. odishaensis*, was described by Baliarsingh et al. (2017); they mentioned Roberts' (1989) comment but did not discuss the generic status of the five species of *Parapsilorhynchus*. None of the species placed in *Parapsilorhynchus* have yet been included in a molecular analysis.

Baliarsingh et al. (2017) figured the mouth of three species. Their figure of *Paraps. discophorus* shows a fish with a very small gular disc, but details cannot be seen from the picture; it has tubercles on the snout, of which the two located anteriorly on the side of the snout are larger (the picture is in ventral view and does not allow further comments on the tubercles). The figure of *Paraps. tentaculatus* shows a bilobed papillated labial fold somewhat reminiscent of *Paracrossochilus vittatus* figured here (especially Fig. 19b). Earlier authors had not reported or figured tubercles in any species of the genus. Baliarsingh et al. (2017) described *Paraps. odishaensis* as having a "poorly developed callous pad behind lower lip, which is not sharply delimited posteriorly", many tubercles on the snout, "of which two are larger, more prominent, located at anterior sides of snout" and three or four unbranched pectoral-fin rays. The figure shows a wide, rounded papillated labial fold, with a triangular structure in the median area of the posterior half, somehow reminiscent of the gular pad mentioned under *Paracrossochilus vittatus*. Singh (1994) reported that in *Paraps. elongatus* the "lower lip [is] bilobed with a small callous thickening behind it". Hora & Misra (1938) reported that in *Paraps. prateri* "behind the lower lip, which is slightly emarginate, there is a callous area of the skin".

Besides the number of unbranched pectoral-fin rays (2–5) there do not seem to be many characters to suggest that the five species of *Parapsilorhynchus* are closely related. Lundberg & Marsh (1976) reviewed the anatomy of pectoral rays in cyprinoid fishes and, among the species of Cyprinidae that they examined, found that all had a single unbranched pectoral-fin ray, except for *Garra*, which has two. The presence of two unbranched rays in African *Garra* is also reported by Stiassny & Getahun (2007: 51) and Kullander & Fang (2004: 277). That the specimens of *Paraps. discophorus* and *Paraps. odishaensis* have well developed tubercles suggests they are possibly adults and that the presence of additional unbranched rays is not a juvenile feature.

Convergent regression vs. convergent evolution of the disc in garras. A number of Southwest Asian and African cyprinids without gular disc earlier placed in *Hemigrammocapoeta*, *Iranocypris*, *Tylognathoides*, *Typhlogarra* and *Phreatichthys* have recently been placed in *Garra* (e.g., Geiger et al., 2014; Hamidan et al., 2014; Hashemzadeh Segherloo et al., 2016). Hashemzadeh Segherloo et al. (2016) commented that "species without a mental disc that former-

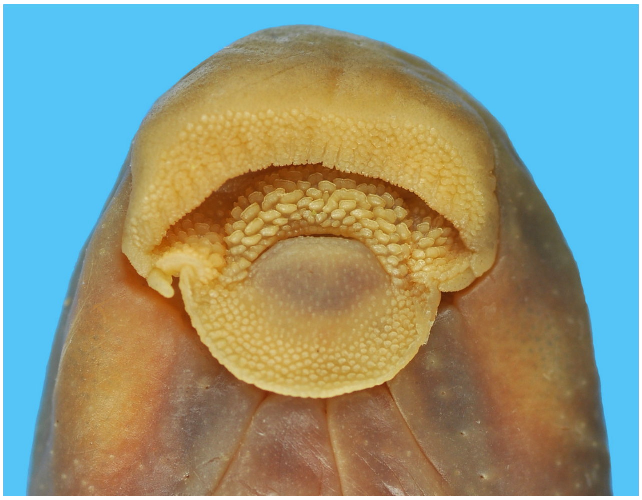

Fig. 25. *Garra variabilis*, CMK 18900, 94.9 mm SL; Turkey: Euphrates drainage.

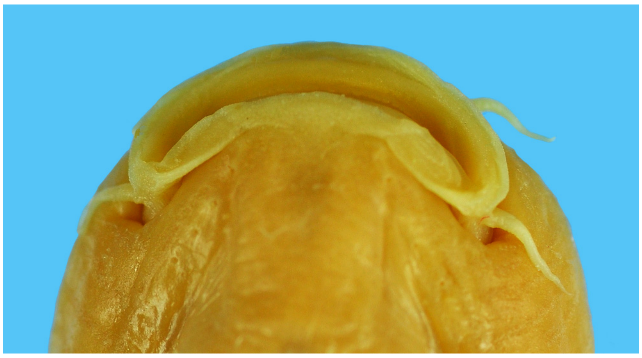

Fig. 27. *Phreatichthys andruzzii*, CMK 7247, 49.2 mm SL; Somalia: Gal Ef cave.

Fig. 26. *Hemigrammocapoeta culiciphaga*, CMK 18795, 54.1 mm SL; Turkey: Ceyhan drainage.

ly had been placed in the genera [...] *Crossocheilus*, *Gonorhynchus* [...] have later been moved to the genus *Garra*". *Gonorhynchus* in fact is *Tariqilabeo* and *Akrokolioplax* (see Kottelat, 2016). I do not know of authors who treated species of *Crossocheilus*, *Tariqilabeo* and *Akrokolioplax* as belonging to *Garra*, except for '*Tylognathus*' *klatti*, which had been listed as a *Crossocheilus* (e.g., Fricke et al., 2007: 38, Çiçek et al., 2015: 144) without mention of a source or of information that would be diagnostic of *Crossocheilus*. Later, Küçük et al. (2015: 362) and Çiçek et al. (2016: 117) treated it as a synonym of *Garra kemali* and Freyhof (2016: 500) as a valid species of *Garra*.

Several of these works, especially Hashemzadeh Segherloo et al. (2016), discuss convergent regression vs. convergent evolution of the disc in Southwest Asian species of *Garra* and argue for a scenario of convergent regression. The trees published in different papers are partly contradictory although sharing a number of the coauthors and sequences, and one may expect more trees to come. I will not enter into details about the discrepancies. Zheng et al. (2012) had a similar discussion on parallel evolution or regression of the disc within all labeonines, but focussed on Chinese species.

I have seen only few species of Southwest Asian and African *Garra* sensu lato and my comments on the morphology of the disc cannot be very detailed. The disc of African species are figured by Stiassny & Getahun (2007) but the details I have mentioned above when introducing the new terminology cannot be recognised. Hashemzadeh Segherloo et al. (2016) discussed "convergent reduction of the mental disc" in Southwest Asian garras. The authors identify the disc as a "specialisation of the lower lip" but do not provide a single word describing the actual morphology of the disc although the (non) development of the disc is the core issue of the paper (being understood that 'fully developed', 'well developed', 'reduced' are not informative since they are not defined; furthermore the wording has an ambiguous teleological content). Their figure 3 shows *G. variabilis* with a 'reduced' disc and *G. festai* (earlier '*Tylognathus*' *festai*) without disc; the figures do not allow to observe details of the disc and lower lip. I do not think it is appropriate to qualify the disc of *G. variabilis* as 'reduced'; it is more appropriately called 'different'. In the specimens I examined (Fig. 25), the pulvinus is smaller than in many other species, thick, soft, swollen while in most garras it is flat and harder. It is separated from the torus by a deep groove and appears as if pushed forwards against the torus. The torus is wide (proportionately wider than in any garra known to me, about as large as the pulvinus), thick, soft, covered with large, flattened, chisel-shaped papillae leaving grooves between them. The pulvinus can be covered by small papillae, about similar to those on the labrum. The width, thickness and ornamentation of the torus and the swollen pulvinus are not a reduced version of what is observed in other species of *Garra*; they cannot be termed a reduced disc, but represent a different disc morphology. Without access to material or adequate illustrations, I cannot comment on the 'absence' of disc in '*G*'. *festai*.

In a similar discussion of possible convergent reduction of the disc, Behrens-Chapuis et al. (2015) did not provide more information on what they considered a reduced or lost disc. In all these discussions, there is no description of the morphology of the mouth and gular region of the species in which the disc is 'lost'. Are they the same in all species that 'lost' the disc or are the resulting morphologies different in the different clades?

Küçük et al. (2015) figured the mouth of *Hemigrammocapoeta menderesensis*, *H. kemali* and *H. culiciphaga* (type species). They were apparently unaware of the recent works that considered the genus as polyphyletic and that placed the different species of *Hemigrammocapoeta* in different lineages within *Garra* sensu lato. Geiger et al. (2014), Hashemzadeh Segherloo et al. (2016) and others retrieved *H. menderesensis* and *H. kemali* as sister group to *G. variabilis*. Several of the features of *G. variabilis* can be recognised in the figures of *H. kemali* and *H. menderesensis* (e.g., the fleshy rostral cap, the wide and fleshy anterior edge of the labial fold) and the hypotheses of a reduction of the elements of the mouth of *G. variabilis* into those of the mouth of *H. kemali* and *H. menderesensis* or the convergent evolution of more or less analogous discs as in other clades are both equally plausible.

On the other hand, the mouth of *H. culiciphaga* (type species of the genus) differs from that of all other examined *Garra* sensu lato in having a structure that appears as a narrowly interrupted 'lower lip' (Fig. 26). However, from the specimens I could examine, it is not possible to conclude whether this structure is really a lip (in which case the free anterior edge of the labial fold would be restricted to the triangular tissues between the lips) or a highly modified labial fold (torus). At the corners of the mouth this 'lower lip' is connected to a vestigial upper lip. This structure is already present, with the same morphology in a specimen 29.0 mm SL (CMK 18795). Younger individuals are needed to determine the identity and ontogeny of these structures.

It is difficult to recognise homologies between the different elements in the mouth structure of *H. culiciphaga* and those that could result from the regression of a *Garra* disc. Besides, *H. culiciphaga* has a body shape that differs from all other garras, its mouth is subterminal (vs. conspicuously inferior), and the colour pattern is made of a broad dark band ending in a black spot at the base of the caudal fin. Noteworthy is that *H. culiciphaga* is part of a clade that includes *G. caudomaculata*, *G. festai*, *G. nana* and *G. sauvagei*, all without gular disc (Freyhof, 2016). Because of lack of material, I have not researched characters potentially usable to diagnose this clade. Under the dogmas of monophyly and of nomenclature strictly reflecting the branching pattern of trees, recognising (naming) *Hemigrammocapoeta* as a valid genus would require naming a number of other clades as distinct genera.

Yang et al. (2012) recovered *Phreatichthys andruzzii*, a cave fish without disc from Somalia, within *Garra*, as sister-group to a lineage including all the African garras they examined plus *G. rufa* from Southwest Asia. In the specimens I examined, the gular area does not show peculiar structures (Fig. 27), the lower lip is present along the lateral third of the lower jaw, and the rostral cap is distinct along the central third, with a narrow margin of a few papillae in some specimens. Vertical rows of sensory pores are present on the posterior half of the side of the head. Regression of various structures is recurrent in cave-adapted fish species and it is difficult to comment without information and material of the epigean species inhabiting the area.

That some forms of disc are present in distantly related genera of Garrina and 'semilabeonina' has been interpreted as evidence that the disc is a plesiomorphic feature of this lineage and has been lost several times during evolution (e.g., Zheng et al., 2012; Geiger et al., 2014; Behrens-Chapuis et al., 2015; Hashemzadeh Segherloo et al., 2016). However, there is no disc in any of the species of 'osteochilina' (the sister group of 'semilabeonina'), and in both Garrina and 'semilabeonina' there are genera/lineages with very complex and sophisticated structures of the gular and oral areas that cannot be all seen as a regressed gular disc (see figures in Gan et al., 2017). To have analogous disc-like structures evolve independently in several lineages (and later regressing in some of them) is certainly at least as parsimonious as to postulate the plesiomorphic presence of a disc in Garrina + 'osteochilina' + 'semilabeonina' that would have regressed in parallel in most lineages to result in simplified structures and/or develop another complex structure. It is at least as likely that all these varied structures evolved independently from basal forms with simple mouth and gular structures and that some structures (or very similar structures) appeared several times. The comparison of the ontogeny of the gular disc in *Garra* sensu stricto (Fig. 15) and *Ageneiogarra* (Fig. 16) clearly shows different developmental origins and steps in the formation of the gular disc.

Outside the Southwest Asian Garrina, the trees resulting from the analyses by Yang et al. (2012) and Zheng et al. (2012) do not demonstrate that the character states called 'disc', 'incomplete disc' or 'absence of disc' are homologous in the various lineages. It is difficult to conceive that a complex structure like the disc would be a plesiomorphy for three of the four clades of Labeonini and would be regressed and lost in species or genera in all clades to result independently in the same (?) simple and quite trivial structure. A structure like a simple labial fold, not differentiated anteriorly, with or without gular grooves, and with thickened gular tissues over the basihyal forming a precursor of the gular pad, is more likely to be the plesiomorphic state. This structure is present in these three clades, in the sister-groups of all lineages in which disc-bearing species are known in South, Southeast and East Asia, and in the whole 'osteochilina'. This basic structure is present (1) in *Tariqilabeo* and *Akrokolioplax*, sister-group of all *Garra* sensu stricto; (2) in *Mekongina* and *Altigena*, in the clade including *Ageneiogarra* and *Placocheilus*; (3) in several genera (e.g., *Pseudocrossocheilus*) in the clade sister to that including *Discogobio* and *Discocheilus*; and (4) in a more elaborate way in *Paracrossochilus*, sister to *Ceratogarra*. Disc-like structures (homologous or analogous) could have appeared in some lineages (e.g., *Parasinilabeo*, *Stenorynchoacrum*, *Ptychidio*, *Cophecheilus*, *Hongshuia*) and secondarily disappear in some species. This is certainly more parsimonious than having a complex structure evolve (obligatorily from a simple one) then disappear *x* times to return to a simple basic condition and/or evolve other complex structures. A critical reassessment of the molecular tree against an effective analysis of soundly defined morphological characters is still needed before embarking on conclusions on the evolution of morphological features or ecology. A next batch of new trees will probably bring more alternative phylogenetic hypotheses.

In the case of the pair *Ceratogarra* + *Paracrossochilus*, the regression hypothesis would mean that the disc would have been lost in *Paracrossochilus*. But in *Paracrossochilus* the structure is as complex as that of the disc in *Ceratogarra*, it develops directly, at a relatively larger size/later age, without going through a disc-like structure, while in *Ceratogarra* the disk develops very early. It seems reasonable to hypothesise that *Paracrossochilus* and *Ceratogarra* have independently derived their gular and oral morphology from a shared ancestor instead of seeing one morphology derived or regressed from the other.

Hashemzadeh Segherloo et al. (2016: 56) commented "the question is whether the mental disc was reduced in convergence or developed in convergence". Why would all lineages have needed to follow the same evolutionary path? A much less teleological or deterministic alternative must critically be examined: the absence of a disc is the ancestral condition, but in some taxa or lineages the absence may result from secondary reduction or loss; and a small disc (like in *G. variabilis*) is not automatically 'more developed' or 'more regressed', but simply 'different'. The claim that the structure of the disc "is identical or differs in very minor aspects in all disc-bearing species studied here, as well as *Garra* species from Africa and Asia" is contradicted by a critical examination and by ontogenetic observations.

Conceptual considerations. A discussion based not only on algorithms (whose mathematical implications cannot be explained by most of their users) needs to precede the placing, for example, of *Hemigrammocapoeta* sensu stricto in the synonymy of *Garra* sensu stricto. In the 1970s there was much debate on phenetics (vs. cladism and 'evolutionary taxonomy') and pheneticism was largely rejected on the basis of biological and logical arguments (it describes similarity or distance, not phylogeny). Nowadays, paradoxically, some of the same algorithms are used to produce 'cladograms' resulting from molecular analysis. Alternative hypotheses should be considered, for example the possibility of intergeneric introgression (e.g., as documented by Freyhof et al. [2006] for *Scardinius dergle*).

It emerges also that discussions on 'morphology' within garras should move beyond the oversimplistic 'description' [sic!] of the gular disc as 'presence' or 'absence', 'normal' or 'regressed'. These are not descriptions. Presence, absence or regressed are not character states of a character 'disc', because the disc is not a character of its own, but a complex organ made of the assemblage of various elements, and these elements are the characters to be described and analysed. The same applies to the proboscis, patches of tubercles (as correctly initiated by Nebeshwar & Vishwanath, 2017), etc. Once more species are included in the analyses of characters (morphological, molecular and others) and accurate descriptions are provided, it is predictable that additional genera will/should/must be recognised and that some of the species without disc indeed will be cases of regression within disc-bearing genera. But other species without disc are likely to be distinct lineages, sisters to various lineages with disc.

While *Hemigrammocapoeta* seems to belong to the main clade of garras, it cannot be treated as a synonym of *Garra* sensu stricto that would have a reduced or lost disc, simply for compliance with the molecular-phylogenetic-cladistic doxa. [doxa: "The orchestration of the categories of perception of the social world that, being adjusted to the divisions of the established order (and by this, to the interests of those who dominate it) and common to all the minds structured in conformity to these structures, impose themselves with all the appearances of the objective necessity" (Bourdieu, 1979: 549; my translation).]

The parsimony rhetoric is not really relevant when parsimony is no longer a postulate but erected as an axiom, for convenience, in order to blindly apply algorithms. Having to resort automatically to parsimony as a criterion to decide among alternative explanations implies accepting the possibility that the actual proccess may remain unrecognised because it is too complex and unparsimonious (or: a parsimonious 'lie' is prefered to a complex 'truth'). Besides, the recourse to parsimony and algorithms is an easy way to avoid discussion. It also allows to hide language limitations, a situation of concern. Most scientists today write and read in a foreign language, often not well mastered, and this results in fewer and less critical discussions, in the selection of approaches allowing an easy conclusion rather than an original discussion, and in the low circulation of critical discussions. Numbers are easier to produce and handle than words. Biology simply disappears from biology publications.

It is not possible to refrain from commenting that many "phylogenetic analyses" ignore that 'phylogenetic' is not a homonym of molecular, and that phylogenetic studies existed long before biochemistry. These analyses merely investigate molecular phylogeny and deal very lightly with morphological information. It is a common observation that, in ichthyology at least, many 'integrative' studies pretending to use morphological information are satisfied with the statistical manipulation of a few morphometric values, of low or no interest. Besides, 'integrative taxonomy' is a pleonasm, since taxonomy integrates all available information, by definition.

Comparative material. *Ceratogarra cambodgiensis*: CMK 5189, 3; Thailand: Tapi drainage. — CMK 8188, 2; ZRC 59776, 6, 33.0–78.7 mm SL; ZRC 59876, 3, 63.4–85.9 mm SL; Malaysia: Terengganu. — CMK 10736, 3, 28.3–31.0 mm SL; Thailand: Chao Phraya drainage. — CMK 19851, 14; CMK 19990, 128; CMK 20004, 159; CMK 20005, 165; CMK 21191, 21; Laos: Mekong drainage: Nam Theun watershed. — CMK 23487, 9; Laos: Mekong drainage: Xe Kong watershed. And about 155 additional lots (3000 specimens) examined in CMK and ZRC, and numerous more in the field, from throughout Mekong drainage in Laos, Thailand and Cambodia (Se San, Xe Kong, Xe Don, Xe Banghiang, Xe Bangfai, Nam Kading, Nam Xan, Nam Ngiep, Nam Mouang, Nam Ngum, Nam Heung, Nam Khan, Nam Xuang, Nam Ou, Nam Beng, Nam Tha, Nam Ma and Nam Youan watersheds), Chao Phraya drainage and Malay Peninsula.

C. fasciacauda: All from Mekong drainage, from South to North: CMK 15711, 2; CMK 21299, 12; Laos: Xe Kong watershed. — CMK 15889, 1; Laos: Mekong mainstream below Khone Falls. — CMK 13455, 1; CMK 13509, 1; CMK 13759, 18; Laos: Xe Banghiang watershed. — CMK 12322, 2; CMK 19307, 3; CMK 23089, 4; CMK 23929, 1; Laos: Xe Bangfai watershed. — CMK 23534, 1, 49.7 mm SL; Laos: Nam Ngum watershed. — ZRC 39306, 3, 73.3–77.8 mm SL; Thailand: Mekong at Nong Khai. — CMK 16094, 2; Thailand: Mekong drainage in Chiangrai Province. — CMK 23940, 1, 71.4 mm SL; China: Xishuangbanna.

Paracrossochilus acerus: All from Borneo: CMK 4809, 2; Barito drainage. — CMK 10590, 1, 42.8 mm SL; CMK 11696, 17; Kapuas drainage. — CMK 21793, 6; CMK 21824, 15; CMK 21892, 1; Mahakam drainage. — CMK 10836, 2; CMK 10848, 1, 55.5 mm SL; ZRC 46764, 88, 40.8–72.9 mm SL; ZRC 46777, 9; ZRC 60455, 51; Sarawak.

P. vittatus: All from Borneo: CMK 10564, 1; CMK 11527, 1, 49.0 mm SL; Kapuas drainage. — CMK 10831, 1, 63.9 mm SL; CMK 10918, 1; Sarawak. — ZRC61131, 8, 44.0–65.0 mm SL; ZRC 61132, 27, 20.0–57.5 mm SL; Katingan drainage.

In addition, material of the following 42 named species of garras has been examined:

Ageneiogarra cyclostomata, *A. imberba*, '*A*'. *micropulvinus*, *A. poilanei*, *A. theunensis*;
Discogobio tetrabarbatus, *D. yunnanensis*;
Garra annandalei, *G. borneensis*, *G. bourreti*, *G. ceylonensis*, *G. cyrano*, *G. dulongensis*, *G. flavatra*, *G. fluviatilis*, *G. fuliginosa*, *G. gotyla*, *G. gracilis*, *G. gravelyi*, *G. hughi*, *G. kempi*, *G. lamta*, *G. lissorhynchus*, *G. macclellandi*, *G. mirofrontis*, *G. mullya*, *G. nasuta*, *G. nigricollis*, *G. notata*, *G. orientalis*, *G. paralissorhynchus*, *G. poecilura*, *G. rakhinica*, *G. robertsi*, *G. rufa*, *G. salweenica*, *G. spilota*, *G. variabilis*, *G. vittatula*;
Hemigrammocapoeta culiciphaga;
Phreatichthys andruzzii;
Placocheilus caudofasciatus.

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