Taxonomy of the genus *Oriverutus* Siddiqi, 1971 (Nematoda: Dorylaimida: Nordiidae)

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After introducing its history, the most relevant morphological features of *Oriverutus* are explained, illustrated (light and scanning electron microscope pictures) and discussed. The taxonomy of the genus is analysed based on the study of all the nominal species, and an emended diagnosis is provided. Its relationships with the closest genera are discussed, and some reflections are made on its phylogeny. *Ecanema* and *Mammillonema* are confirmed as junior synonyms of *Oriverutus*, *Inbionema* is regarded as its junior synonym also, whereas *Paroriverutus* is considered to deserve separate generic status. Consequently, several nomenclatorial changes are derived: *Paroriverutus ivorensis* is retained under *Paroriverutus*, *Drepanodorylaimus macramphidius* and *Oriverutus longicaudatus* are transferred to *Paroriverutus*, and *Inbionema biforme* to *Oriverutus*. An updated list of *Oriverutus* species is provided as well as a key to the identification of its didelphic species and a compendium of their morphometrics.

Keywords: compendium; key; morphology; nomenclatorial changes; species list; systematics

Introduction

The genus *Oriverutus* Siddiqi, 1971 is an interesting dorylaimid taxon for several reasons. With 35 valid species, it is a medium-rich nematode group, although recent contributions (see below) suggest that its diversity is certainly much higher than either known or expected. Its geographical distribution shows a rather special pattern because its representatives mainly inhabit tropical areas of at least three continents (Africa, America and Asia) and two islands or archipelagos (Papua New Guinea and Mauritius), being occasionally found in temperate regions (Korea, Japan, Spain). Morphologically, *Oriverutus* is a well-characterized genus, distinguishable by a peculiar combination of features: lobe-like lips, odontostyle relatively long and slender with short aperture, pharyngo-intestinal junction often bearing three cardiac cells, and tail conically elongated usually with more or less (but always perceptible) bent dorsad end. Nevertheless, its evolutionary relationships are far from being well elucidated. Originally (Siddiqi 1971) classified under Qudsianematidae Jairajpuri, 1965, it was later (Jairajpuri and Ahmad 1992) accommodated in Nordiidae Jairajpuri and Siddiqi, 1964. After its proposal, several other more or less comparable genera have been described. Leaving aside some morphological variability affecting the lip region, odontostyle and female genital system (mono-opisthodelphic or

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didelphic), the separation of *Oriverutus* species is mainly based on morphometrics and becomes intricate.

The aim of this contribution is to re-evaluate the taxonomy of the genus in the light of new findings, especially those derived from scanning electron microscope (SEM) observations of the lip region.

Material and methods

An exhaustive literature review was carried out to compile all the information published about didelphic species of the genus, whereas that provided by the own authors in a recent contribution (Peña-Santiago et al. 2013) is used for monopisthodelphic species. Type material and/or voucher specimens of many *Oriverutus* species earlier described by the authors (see list of references) were available to study. In addition, material of four genera very similar to *Oriverutus* was re-examined for comparative purposes: one female of *Ecanema ecae* previously studied by Liébanas et al. (2011), one female and one male paratype of *Inbionema uniforme* as well as two female paratypes and one male paratype of *Parapalus arboricola*, deposited in the nematode collection of the University of Jaén (Spain), and three female paratypes of *Oriverutoides attenuatus* belonging to the German Nematode Collection (Biologische Bundesanstalt, Münster, Germany). Nematodes were observed and photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS.

Historical outline

Siddiqi (1971) erected the new genus *Oriverutus* to accommodate the new and type species, *O. lobatus*, and four known ones transferred from other genera: *Oriverutus hastatus* (Andrássy 1963) and *Oriverutus impar* (Khan and Khan 1964) from *Longidorella* Thorne, 1939; *Oriverutus hastulatus* – new name for *Tylencholaimus hastatus* Siddiqi, 1964a – from *Tylencholaimus* de Man, 1876; and *Oriverutus sundarus* (Williams 1964) from *Eudorylaimus* Andrássy, 1959. The new genus was classified under the family Qudsianematidae and separated from *Eudorylaimus* “in having larger amphids, attenuated spear, different shape and position of the dorsal oesophageal gland nucleus, a long dorsal oesophageal gland duct, anterior position of the outlets of the subventral glands in the oesophageal enlargement and the characteristic glandular tissue around the oesophago-intestinal valve” (Siddiqi 1971, p. 485). *Oriverutus* was also originally compared with *Poronenemella* Siddiqi, 1969, but distinguished from this by its “polymyarian somatic musculature, indistinct body pores, large amphids and attenuate spear”.

Andrássy (1976) maintained *Oriverutus* under Qudsianematidae, subfamily Qudsianematinae. Several new species of the genus were described during the 1980s (Baqri 1980; Ahmad and Jairajpuri 1982, 1987). In their 1992 monograph, Jairajpuri and Ahmad listed 13 valid species, classified *Oriverutus* under the new subfamily Actinolaimoidinae of the family Nordiidae, and regarded the genus *Mammillonema* Darekar and Khan, 1982 as its junior synonym (Jairajpuri and Ahmad 1992). Already in the 1990s, Ahmad and Siddiqi (1997) added four new species to the catalogue and regarded the genus *Paroriverutus* Carbonell and Coomans, 1982 as its junior synonym. New contributions to the diversity of the genus appeared during the last decade. Andrássy (2002) listed 21 species, two of them new, and gave a key to

their identification; besides, this author provided an emended diagnosis of the genus, which was again maintained under Nordiidae, and discussed its affinities with *Actinolaimoides* Meyl, 1957 and *Malekus* Thorne, 1974. Ahmad and his collaborators (Ahmad and Ahmad 2002; Ahmad and Araki 2002; Ahmad and Shaheen 2003; Ahmad 2007; Baniyamuddin and Ahmad 2007) described several new species. Andrssy (2009) mentioned that *Oriverutus* included 27 species (although their list was not provided by the author), classified it under the new subfamily Oriverutinae, regarded *Ecanema* Ahmad and Shaheen, 2005 as its junior synonym, and mentioned that *Inbionema* Loof and Zullini, 2000 might be identical to it. Libanas et al. (2011) and Libanas and Pea-Santiago (2011) studied six (three new and three known) species from Costa Rica. And, very recently, Pea-Santiago et al. (2013) provided a revision of the 13 opisthodelphic *Oriverutus* species, three of them being new.

Main morphological features and their taxonomical interest

Lip region and amphids

As observed using light microscopy (Figure 1), it appears offset from adjacent body by a more or less marked depression, occasionally a constriction (Figure 1D). It is

Figure 1. Lip region of *Oriverutus* species in median, lateral view (light microscopy). (A) *Oriverutus andrassyi* Pea-Santiago et al., 2013; (B) *Oriverutus asaccatus* (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987; (C) *Oriverutus belloi* Libanas et al., 2011; (D) *Oriverutus costaricensis* Libanas and Pea-Santiago, 2011; (E) *Oriverutus hemihystera* Libanas and Pea-Santiago, 2011; (F) *Oriverutus kalikus* Gambhir et al., 2008; (G) *Oriverutus sundarus* (Williams 1964) Siddiqi, 1971; (H) *Oriverutus tropicus* Ahmad and Shaheen, 2003. Scale bars: A–F, H = 10 µm; G = 5 µm.

very often visibly but moderately expanded, i.e. slightly wider than the adjacent body region. Its general profile is comparatively high since the lip region is only about 2.5 times as wide as high, and very angular. The lips are conspicuously separated, with distinctly protruding labial and cephalic papillae. And the perioral area is also characteristically elevated and projecting, nearly reaching the level of lip tips. The amphid aperture is large, occupying about three-quarters of the lip region diameter. This pattern is typical of the genus, present in most of its representatives. Nevertheless, some species show some variations especially regarding the height and separation of lips and/or the protrusion of their papillae.

Observations by SEM (Figures 2 and 3) confirm those obtained with light microscopy and allow a better explanation and understanding of the nature of the lip region. Lips are high, lobe-like, and totally separated by the existence of deep radial incisures. Lateral lips are appreciably larger than the subdorsal and the subventral ones, especially at their base. Both subdorsal lips and both subventral lips are visibly separated between them and closer to their respective lateral lip, so it is possible to divide the lip region into two sides (left and right; easily perceptible in Figure 2E). Labial and cephalic papillae are button-like, always protruding on the surface of lips. Perioral area is also high, lobe-like and projecting, reaching the level of lip tips, and, as seen in frontal view, it seems a central, oval, dorsoventral, ring-like structure, separated from the lips by a well-marked circular incisure. The oral aperture is a short dorsoventral slit surrounded by the central lobe. Hence, the lip region shows a discernible bi-radial symmetry. Amphid aperture is a large transverse slit, nearly running the lip region width.

When proposing *Oriverutus* as new genus, Siddiqi (1971; see also Jairajpuri and Ahmad 1992) did not emphasize the morphology of the lip region to characterize this taxon, but Andrssy (2002, 2009) did. Despite SEM pictures only being available for a few species, the observed lip region pattern is probably common within the genus, but further species should be studied with SEM to elucidate the variability affecting this character. Especially remarkable for this pattern are the bi-radial symmetry and the shape adopted by the perioral area: a protruded, lobe-like structure, distinctly delimited or separated from the lips. This pattern certainly supposes an apomorphic condition and the most characteristic diagnostic feature of the genus.

Odontostyle

It is attenuate, i.e. relatively long, slender and with small aperture (Figure 1). Always exceeding the lip region diameter, the odontostyle length usually varies from 10 to 25 μm or 1.2 to 2.5 times the lip region width. It is often at least 10 times as long as wide and its aperture, not always well visible, very frequently occupies less than one-fifth of total length, but occasionally may be larger (Figure 1H).

Odontostyle morphology is used as a relevant diagnostic feature of the genus, especially to establish its evolutionary relationships (see below).

Pharynx

It is typical dorylaimoid, consisting of a slender but muscular anterior section that enlarges gradually, and a moderately developed basal expansion that very often

Figure 2. Lip region of *Oriverutus* species (scanning electron microscopy). (A, D) *Oriverutus asaccatus* (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987; (B, E) *Oriverutus sundarus* (Williams, 1964) Siddiqi, 1971; (C, F) *Oriverutus tropicus* Ahmad and Shaheen, 2003; (G-I) *Oriverutus occidentalis* Peña-Santiago and Peralta, 1991. A–C: Sublateral or ventral view; D–E: frontal view. Scale bars 5 μ m.

occupies two-fifths to one-half of total neck length, seldom exceeding this range. Pharyngeal gland nuclei are often small and not too much conspicuous: DN is located at an appreciable distance from DO; S_1 N are especially small and difficult to observe, but they are well apart and located at the anterior half of the basal expansion; and S_2 N are found far from the pharyngeal base at about 85–90% of total neck length.

Figure 3. Lip region of *Oriverutus* species (drawing based on scanning electron microscope pictures). (A, D) *Oriverutus asaccatus* (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987; (B, E) *Oriverutus sundarus* (Williams 1964) Siddiqi, 1971; (C, F) *Oriverutus occidentalis* Peña-Santiago and Peralta, 1991.

Pharyngo-intestinal junction

It displays relevant and interesting diversity (Figure 4). A more or less developed (often small) valve-like structure (the cardia) is always present. In a few species (for example, *O. belloii*, *O. papillatus* and *O. tropicus*) the cardia is asymmetrical – its dorsal side bulges in a perceptible lobe (Figure 4A, B). Most species bear three cardiac cells (Figure 4C–E). And several forms have a dorsal cell mass just behind the cardia level and/or at the anterior end of intestine (Figure 4F). These variations (asymmetry, cardiac cells and dorsal cell mass) should be regarded as apomorphic conditions of their respective characters, but, not being present in all the species, their value as diagnostic features to define and to distinguish the genus is questionable. The absence of cardiac cells might be interpreted as a secondary loss.

Female genital system

Thirteen species are mono-opisthodelphic whereas the remaining are didelphic–amphidelphic. Among amphidelphic species, *O. hemihystera* has the anterior genital branch less developed (but apparently functional) than the posterior one. Most

Figure 4. Pharyngo-intestinal junction in *Oriverutus* species (light microscopy). (A) *Oriverutus belloï* Liébanas et al., 2011, showing a dorsal lobe of cardia (arrow head); (B) Same in *Oriverutus tropicus* Ahmad and Shaheen, 2003; (C) *Oriverutus asaccatus* (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987, showing cardiac cells (arrow head); (D, E) Same in *Oriverutus sundarus* (Williams 1964) Siddiqi, 1971; (F) *Oriverutus ecae* (Ahmad and Shaheen 2005) Andrassy, 2009. Scale bars: A–D = 10 μ m.

opisthodelphic species totally lack a pre-vulval uterine sac (Figure 5A), which occasionally becomes very short (e.g. in *O. tropicus*; Figure 5D); exceptionally, only *O. vanisti* displays a large sac with vestigial oviduct and ovary. The uterus is the most variable structure in the genus, often being simple (Figure 5A), but bipartite (Figure 5B) or tripartite (Figure 5C) in some species; its distal portion, close to the sphincter, occasionally bears special differentiation such as the presence of refractive elements (Figure 5B). The vagina usually consists of *pars refringens*, but this is lacking in a few species (Figure 5E). The vulva is a transverse slit, but pore-like in *O. lobatus*.

Variation observed in the morphology of the female genital system is very useful to characterize and separate *Oriverutus* species, but it does not show any regular pattern.

Male genital system and accessory elements

Males are known only in two of the 13 opisthodelphic species: *O. vanisti* has males as frequent as females, and a unique male specimen has been reported for *O. sundarus*. In contrast, didelphic species often have both females and males equally frequent. As

Figure 5. Female genital system of *Oriverutus* species (light microscopy). (A) *Oriverutus asaccatus* (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987; (B) *Oriverutus ecae* (Ahmad and Shaheen 2005) Andrassy, 2009 (arrow head pointing at refractive elements inside distal part of uterus); (C) *Oriverutus tropicus* Ahmad and Shaheen, 2003; (D) *Oriverutus sturhani* Ahmad and Shaheen, 2003; (E) *Oriverutus istvani* Peña-Santiago et al., 2013. Scale bars: A–C = 10 μ m; D, E = 5 μ m.

usual, no relevant intrageneric variation is observed in the morphology of the male genital system, but secondary sexual structures show some interesting differences. In addition to the ad-cloacal pair, there is a series of one to eleven, more or less regularly spaced, ventromedian supplements, which are often located outside the range of spicules (i.e. hiatus is present), but that in two cases, namely *O. anisi* and *O. arcuatus*, the posteriormost are situated at the level of the anterior end of spicules or slightly within their range, and in three species (*O. ecae*, *O. masculus* and *O. maturitatis*) lack hiatus and have one to three ventromedian supplements within the range of spicules. Spicules are relatively small, ranging from 22 to 40 μ m long, and weakly sclerotized.

The number and arrangement of ventromedian supplements are also useful to characterize and separate species, but do not follow a definite pattern. Spicules do not provide much interesting information for taxonomic purposes.

Caudal region

It is always conical with more or less rounded terminus, basically similar in both sexes (Figure 6). Its most significant variation affects its curvature and its size (length). In many species the ventral side of tail is nearly straight (Figure 6B, C, H) or slightly curved ventrad (Figure 6A, E), whereas the dorsal side appears regularly convex (Figure 6E) but very often with a more or less developed (almost always easily perceptible) terminal concavity (Figure 6A–C, G). Several species, however, show regularly and visibly curved ventrad caudal region (Figure 6D, F). The inner core of tail may reach the tail tip (Figure 6A, G), but, more often, it does not reach the tip and a more or less developed hyaline, terminal portion is easily perceptible (Figure 6B, D, E, H).

Figure 6. Caudal region of *Oriverutus* species (light microscopy). (A) *Oriverutus asaccatus* (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987; (B) *Oriverutus belloi* Liébanas et al., 2011; (C) *Oriverutus costaricensis* Liébanas and Peña-Santiago, 2011; (D) *Oriverutus ecae* (Ahmad and Shaheen 2005) Andrassy, 2009; (E) *Oriverutus hemihystera* Liébanas and Peña-Santiago, 2011; (F) *Oriverutus microdorus* Ahmad and Siddiqi, 1997; (G) *Oriverutus vanisti* Peña-Santiago et al., 2013; (H) *Oriverutus sundarus* (Williams 1964) Siddiqi, 1971. Scale bars: 10 µm, except G = 20 µm.

Tail shape and size show relevant intrageneric, but also some intraspecific, variation, and should be taken with caution to characterize the genus and to separate its species.

Taxonomy

Emended diagnosis

Small- to medium-sized nematodes, 0.56–2.21 mm long. Cuticle with two, occasionally three, layers. Lip region high, with bilateral symmetry: lips distinctly separate,

lobe-like, the lateral ones larger than the subdorsal and subventral; papillae visibly protruding on the surface of lips; perioral area an elevated (also lobe-like) structure, well demarcated from the adjacent lips and surrounding the oral aperture, which is a dorsoventral slit. Amphid aperture occupying most of lip region diameter. Odontostyle attenuate, 10–26 (39–66 in *E. biformis*) μm long and longer (up to three times) than lip region diameter; aperture small, usually up to one-fifth its length, exceptionally larger. Guiding ring simple. Odontophore rod-like. Pharyngeal expansion occupying up to one-half of total neck length. Cardia symmetrical or asymmetrical, bearing or not three cardiac cells. Female genital system didelphic–amphidelphic or monodelphic–opisthodelphic. *Pars refringens vaginae* usually present, seldom absent. Uterus often simple and short, occasionally bi- or tri-partite. Vulva transverse (pore-like in *O. lobatus*), often pre-equatorial. Male with one to twelve spaced ventromedian supplements, with or without hiatus. Tail similar in both sexes, conical, more or less curved ventrad, often slightly bent dorsad at the end.

Relationships

Three genera, namely *Ecanema*, *Mammillonema* and *Paroriverutus*, are very similar to *Oriverutus* and have been regarded as its junior synonyms by Andrssy (2009); Jairajpuri and Ahmad (1992), and Ahmad and Siddiqi (1997), respectively. *Inbionema* is almost identical (cf. Andrssy 2009), and *Oriverutoides* Ahmad and Sturhan, 2002 and *Parapalus* Loof and Zullini, 2000 are very close to it. Besides, in its general morphology, especially the comparatively long and slender odontostyle, *Oriverutus* resembles *Dorydorella* Andrssy, 1987, *Kochinema* Heyns, 1963 and *Longidorella* Thorne, 1939. A comparative analysis of *Oriverutus* with its relatives is presented here.

Ecanema

When originally proposed, this genus had *E. ecae* as its type and only species, Ahmad and Shaheen (2005) distinguished it from *Oriverutus* on the basis of three main differences: the tripartite (versus bipartite) nature of pharynx, S_1N_1 of similar (versus dissimilar) size as DN, and absence (versus presence) of hiatus. Andrssy (2009) regarded *Ecanema* as a junior synonym of *Oriverutus*, stating that (p. 375) “neither the oesophageal structures nor the position of the supplements show any differences between these genera”. Libanas et al. (2011) studied in detail one female of *E. ecae* (reported as *Oriverutus ecae*) from Costa Rica and found that it fits the *Oriverutus* pattern very well, especially regarding the most characteristic feature of this genus, the lip region morphology (Figures 1F and 7A), hence accepting Andrssy’s (2009) criterion. Nevertheless, *O. ecae* is a peculiar member of *Oriverutus* by having especially slender (but not non-muscular, as originally described) anterior portion of pharynx, a comparatively long pharyngeal enlargement with a characteristic narrowing (Figure 7E), and refractive elements at the distal portion of uterus, close to the sphincter (Figure 5B), but these characters should be interpreted as intrageneric rather than intergeneric variations. Regarding the size of S_1N_1 compared with DN, a re-examination of the female of *O. ecae* studied by Libanas et al. (2011) confirmed that S_1N are larger than S_2N and that S_1N are more or less similar in size to DN (Figure 7B–D); nevertheless, an identical scheme occurs in other *Oriverutus* species,

Figure 7. Morphological features of *Oriverutus ecae* (Ahmad and Shaheen 2005) Andrassy, 2009 (= *Ecanema ecae*) (light microscopy). (A) Anterior region in median, lateral view; (B–D) Pharyngeal expansion, with arrow heads pointing at pharyngeal gland nuclei: DN in (B), S_1N_1 and S_2N_1 in (C), and S_1N_2 and S_2N_2 in (D); (E) Pharyngeal enlargement, with arrow head pointing at DN. Scale bars: A = 5 μm ; B–E = 20 μm .

for instance in *O. tropicus*, as revealed by the re-examination of well-preserved specimens of this species. Obviously, the absence of hiatus in *O. ecae* is not a relevant difference because at least two other *Oriverutus* species bear ventromedian supplements within the range of spicules (see above). Hence, Andrassy's action, synonymising *Ecanema* with *Oriverutus*, is solidly founded and well justified.

Mammillonema

Darekar and Khan (1982) described the new genus *Mammillonema*, with *M. mammillatus* as its type and unique species, and compared it to *Oriverutus*, from which it was separated by a series of seriously questionable differences: mammillate papillae, nature of odontophore ("spear extension asymmetrical, zig-zag anteriorly"), both pharyngeal regions nearly equal in length, female genital system didelphic, and mammillate ventromedian supplements. Only the differences observed in odontophore nature might be of some taxonomical relevance, but such a "zig-zag" design has not been described in dorylaeids, and is often the result of inadequate killing and fixation processes. Jairajpuri and Ahmad (1992) regarded *Mammillonema* as identical to *Oriverutus* and transferred its only and type species to the latter, an action that seems to be well justified and herein accepted.

Paroriverutus

This genus was described by Carbonell and Coomans (1982), with *P. ivorensis* from the Ivory Coast as its type and only species. The new taxon, morphologically close to *Oriverutus*, was separated from this (p. 899) “in having a longer odontostyle, more posterior position of guiding ring, more posterior position of S_1N_1 and S_1O_2 , less developed glandular tissue at the pharyngo-intestinal junction and much longer tail”. After describing three new *Oriverutus* species with comparatively long odontostyle, weakly developed glandular tissue near the cardia and/or conical elongate caudal region, Ahmad and Siddiqi (1997) considered that differences between both genera were not enough to maintain separate generic status, synonymised *Paroriverutus* with *Oriverutus*, and transferred *P. ivorensis* to *Oriverutus*. This action was accepted by Andrassy (2002, 2009). The excellent original description of *Paroriverutus* allows re-evaluating and updating its comparison with *Oriverutus*. Three relevant features of this genus, namely lip region hemispherical with completely fused lips, guiding ring double and tail long in both sexes (196–232 μm , $c = 6.2\text{--}6.9$, $c' = 8.4\text{--}9.0$ in females), conform to a morphological pattern that significantly differs from that observed in *Oriverutus* and support the separation of both taxa. Consequently, *Paroriverutus* is considered to be a valid taxon, distinguishable from *Oriverutus* by its lip region hemispherical with amalgamated (versus distinctly separated, lobe-like) lips, double (versus simple) guiding ring, and longer caudal region (> 190 versus < 160 μm).

Andrassy (1971) described the new species *Drepanodorylaimus macramphidius* from Angola, which, three decades later (2002), was transferred to *Oriverutus* by the same author. This species is characterized by, among other features, its lip region with amalgamated lips, double guiding ring and long female tail (152 μm , $c = 8.3$, $c' = 9.5$), which is very similar to those found in *Paroriverutus* pattern.

Oriverutus longicaudatus, originally described by Ahmad and Siddiqi (1997) from Cameroon, is an atypical species within its genus because of its apparently double guiding ring (see Ahmad and Jairajpuri's Fig. 3A) and long tail (108–153 μm , $c = 6.2\text{--}10.6$, $c' = 6.3\text{--}9.5$). Andrassy (2002) regarded it as a junior synonym of *O. macramphidius*, but some relevant differences between the two species can be found to maintain tentatively a separate status for them, for instance neck length [289–386 μm , $b = 3.4\text{--}3.7$ in *O. longicaudatus* ($n = 12$) versus 237 μm , $b = 5.3$ in *O. macramphidius* ($n = 1$)] and vulva position ($V = 48\text{--}51$ versus $V = 53$).

Oriverutus macramphidius and *O. longicaudatus* are very close to *Paroriverutus ivorensis*, having in common the double guiding ring (a relevant feature in dorylaids) and the long tail. Besides, it is also remarkable that these three species are only known to occur in western Africa and might share a recent common ancestor. For these reasons, the former taxa are transferred to *Paroriverutus* as *P. macramphidius* (Andrassy 1971) comb. nov. and *P. longicaudatus* (Ahmad and Jairajpuri, 1997) comb. nov., respectively. Doing so, *Oriverutus* and *Paroriverutus* become more homogeneous taxa, easily distinguishable on the basis of the guiding ring (simple versus double, respectively) and length of tail (< 100 μm , $c < 10$, $c' > 5$ versus > 100 μm , $c < 10$, $c' > 6$). Another tentative difference between the genera could be the morphology of lip region, but further studies are needed to clarify this matter.

Figure 8. *Inbionema bifforme* Loof and Zullini, 2000 (light microscopy). (A) Anterior region in median, lateral view; (B) Pharyngeal expansion, with arrow heads pointing at pharyngeal gland nuclei; (C) Uterine eggs; (D) Spicules; (E) Lip region Spicules; in surface, lateral view; (F) Male, caudal region; (G) Female, caudal region; (H) Pharyngo-intestinal junction; (I) Ventromedian supplements. Scale bars: A, G = 10 μ m; B, C = 50 μ m; D, F, H, I = 20 μ m; E = 5 μ m.

Inbionema

Loof and Zullini (2000) described the new genus *Inbionema* from Costa Rica, with *I. bifforme* as its type and only species. It was distinguished from *Oriverutus* in body size (more than 1.5 versus under 1.3 mm in *Oriverutus*), the morphology of lip region (lips deeply separate versus partly separate; two circles versus one circle of papillae in lateral view), odontostyle length (> 38 versus up to 18 μ m), arrangement of S_1N (close together versus far apart), cardiac cells (absent versus present), tail length ($c' = 1.1\text{--}1.6$ versus $1.9\text{--}5.6$), and shape of spicules (very thick versus normal). One female and one male paratype, deposited in the nematode collection of the University of Jaén (Spain), were available to study (Figure 8). Light microscope and SEM pictures (see Figure 8A, D and Loof and Zullini's Fig. 6, respectively) show that the lip region of *Inbionema* is totally comparable with that found in *Oriverutus* species (Figure 2 in this contribution), with no significant difference. Regarding the location of pharyngeal gland nuclei, it displays a pattern

(Figure 8B) similar to that observed in some *Oriverutus* species, for instance *O. ecae* and *O. tropicus* (see above). It is now known (see above) that cardiac cells may be either present or absent in *Oriverutus* species. Hence, the main differences between these genera are reduced to morphometrics, since *I. biforme* is significantly larger than *Oriverutus* species, although, taking into consideration the current described diversity for the former genus, such differences are now smaller: body length (1.5–2.2 versus up to 1.26 mm in *O. occidentalis*), odontostyle length (39–66 versus up to 26 μ m in *O. longistylus*) –it is remarkable that Loof and Zullini emphasized that within the same population they found two groups of specimens significantly differing in odontostyle length, 39–43 and 59–66 μ m, without intermediate values–, tail length ($c' = 1.1$ – 1.6 versus $c' = 0.8$ – 1.8 in *O. ecae*), and spicule length (69–85 versus up to 40 μ m in *O. pagarus*). Andrssy (2009) stated (p. 373) that “*Inbionema* strongly resembles *Oriverutus* ... , these genera may be identical”. Taking into account that *Oriverutus* seems to be a highly diverse taxon in Costa Rica, the species described as *I. biforme* might represent one of its evolutionary lines in which the general size suffered an important increase. Then, *Inbionema* is herein considered to be identical to *Oriverutus*, and its only species transferred to the former genus as *Oriverutus biformis* (Loof and Zullini 2000) comb. nov.

Oriverutoides

The only and type species of this genus, *Oriverutoides attenuatus* from New Zealand, resembles some representatives of *Oriverutus* in the morphology of lip region with protruding papillae, attenuate odontostyle, opisthodelphic female genital system and tail shape. Ahmad and Sturhan (2002) originally distinguished it from *Oriverutus* in the more posterior location of DO, DN and amphid aperture (versus more posterior than usual), sclerotized cheilostom and the absence of cardiac cells. Re-examination of type material (three female paratypes) of *Oriverutoides attenuatus* (Figure 9) confirms the resemblance between this species and some representatives of *Oriverutus*. Unfortunately, the differences between them cannot be totally confirmed herein. On one hand, the position of the amphid aperture is quite posterior (Figure 9E, F), more than usually observed in *Oriverutus*, as mentioned by Ahmad and Sturhan (2002); besides, the aperture is a comparatively large oval, not a transverse slit as often occurs in *Oriverutus* species (Figure 2). On the other hand, the location of pharyngeal gland nuclei and their outlets is obscure in the three available specimens; and the existence of sclerotization in the cheilostomatal walls seems questionable since the best preserved female does not show any distinct differentiation in cheilostom (Figure 9A) whereas in another female, in a worse state of preservation, it is possible to distinguish two small granular bodies (Figure 9B) at both sides of the cheilostom, which might represent the inner core of the respective lips. Of course, the absence of cardiac glands is not a difference between *Oriverutoides* and *Oriverutus* (see above). Consequently, and taking also into consideration the geographical distribution of *Oriverutoides*, which is far from the current known range of *Oriverutus*, both genera are provisionally considered as valid and separate taxa.

Parapalus

When proposing this genus, with *Parapalus arboricola* from Costa Rica as its only and type species, Loof and Zullini (2000) classified it under Qudsianematidae,

Figure 9. *Oriverutoides attenuatus* Ahmad and Sturhan, 2002 (female, light microscopy). (A, B) Anterior region in median, lateral view; (C) Pharyngo-intestinal junction; (D) Caudal region; (E, F) Anterior region in surface, lateral view. Scale bars: A, B, E, F = 5 μ m; C = 10 μ m; D = 20 μ m.

Paraxonchiinae due to its neck strongly tapering forwards, the lip region becoming (p. 609) “less than 25% of body diam. at base of pharynx”. *Parapalus* was not compared with *Oriverutus* and its closest genera. The taxonomy of paraxonchiid taxa suffered some changes during the next decade (cf. Baniyamuddin et al. 2010), but the concept and status of *Parapalus* remained invariable. The re-examination of type material of *Parapalus arboricola* has revealed (Figure 10) that the general morphology of this taxon resembles in many aspects to that of *Oriverutus* (lip region visible expanded, odontostyle longer than lip region, conical tail with a weak dorsal concavity), but also confirmed that the neck region strongly tapers towards the anterior end, with very narrow lip region (Figure 10A–C), a remarkable feature indeed. Besides, lips are separated but probably not lobe-like (Figure 10D–F), odontostyle is relatively robust, and the pharyngo-intestinal junction lacks gland cells but the cardia is distinctly asymmetrical (Figure 10G), all these features being unusual but not unknown in *Oriverutus* species. *Parapalus arboricola* might represent an extreme case within the potential variability of the genus *Oriverutus*, but, taking into account that the strong tapering of the neck region is a relevant qualitative apomorphic state, not described in *Oriverutus*, *Parapalus* is accepted as a valid genus, provisionally distinguishable from *Oriverutus*.

Dorydorella

Originally created (Andrássy 1987) to accommodate three *Eudorylaimus* species with comparatively long odontostyle (1.3–2.0 times the lip region diameter), *Dorydorella* is a poorly characterized genus. It resembles *Oriverutus* in its general appearance and

Figure 10. *Parapalus arboricola* Loof and Zullini, 2000 (light microscopy). (A–C) Neck region of female, male and J4, respectively; (D) J4, anterior region in median, lateral view; (E) Male, anterior region in median, lateral view; (F) Male, lip region and amphid fovea in submedian, lateral view; (H) Vagina; (I) Male, spicules and caudal region. Scale bars: A–C = 100 μ m; D–F, H = 5 μ m; G = 10 μ m; I = 20 μ m.

odontostyle length, but both genera are provisionally distinguishable by the morphology of lip region (lips not lobe-like and perioral area barely differentiated in *Dorydorella*) and of female tail (always straight ventrally and up to twice the anal body diameter in *Dorydorella*). Nevertheless, further studies should be undertaken to elucidate the relationships between these two genera.

Kochinema

It can be separated from *Oriverutus* in a peculiar combination of characters: lip region distinctly expanded, much wider than adjacent body, amphid aperture in anterior (labial) position and double guiding ring.

Longidorella

Also bearing a long odontostyle, this genus differs from *Oriverutus* in the morphology of lip region (versus lips not lobe-like and perioral area scarcely differentiated), and larger (versus usually three times the lip region width long or more, but occasionally shorter) and more slender (flexible) odontostyle. Besides, *Longidorella* species are, in general, smaller and stouter; and their tail is conical and regularly curved ventrad, more rarely straight ventrally or conoid to rounded.

Malekus

This taxon and *Oriverutus* have in common the distinctly protruding papillae in lip region and the comparatively long odontostyle. Nevertheless, they differ in the morphology of lips (versus amalgamated in *Malekus*), odontostyle (versus much slender, needle-like), and guiding ring (versus apparently double).

Phylogeny

As they can be derived from available data, and in agreement with the new concept herein proposed, evolutionary relationships of *Oriverutus* become intricate. Originally classified under Qudsianematidae on the basis of its general morphology (Siddiqi 1971), it was later included in Nordiidae because of its relatively long and slender odontostyle (Jairajpuri and Ahmad 1992). However, both families are certainly artificial (polyphyletic) taxa, which lack a convincing morphological characterization and do not find molecular support (Holterman et al. 2008; Pedram et al. 2011), a proof that odontostyle morphology has probably been overestimated in the taxonomy of dorylaims (Dorylaimina) and that brings the question to the general problem of Dorylaimoidea phylogeny.

From the morphological perspective, *Oriverutus* pattern (lips lobe-like, long odontostyle, cardiac cells usually present, mono-opisthodelphy in many species, female tail often conical elongate and bent dorsad at the end, etc.) is easily recognizable and does not compare to others. *Oriverutoides* is very close to *Oriverutus*, but it shows some relevant evolutionary novelties (sclerotized cheilostom, backwards migration of amphid aperture and DN; see above) that make it difficult to assess if either both taxa share a recent common ancestor or the former derives from any evolutionary line within the latter. Biogeographical evidence seems to support the second hypothesis because no *Oriverutus* species has been reported from New Zealand, a country whose nematode fauna is acceptably known. Relationships among *Oriverutus* and *Paroriverutus* (guiding ring double, long tail; see above) might not be as close as assumed, the latter provisionally being a taxon only distributed in western Africa. Also, *Malekus* displays significant differences when compared with *Oriverutus*. Andrassy's action (2009), proposing the new subfamily Oriveturinae to group *Oriverutus* and their relatives (*Inbionema*, *Malekus* and *Oriverutoides*; *Paroriverutus* regarded as identical to *Oriverutus*, see above), is hence not totally justified; it should be taken with caution and be the matter of further analysis. Additional studies are also needed to clarify the relationships of *Oriverutus* with *Longidorella* and, very especially, with *Dorydorella*.

Unfortunately, no molecular data of *Oriverutus* and its closest relatives are available. This poses a major limitation to elucidate their systematics.

List and key to species

Oriverutus currently contains 35 valid species:

Type species:

O. sundarus (Williams 1964) Siddiqi, 1971
= *Eudorylaimus sundarus* Williams, 1964

Other species:

O. andrassyi Peña-Santiago et al., 2013
O. anisi Ahmad and Jairajpuri, 1987
O. arcuatus Baqri, 1980
O. arcuicaudatus Ahmad and Araki, 2002
O. asaccatus (Dhanachand and Jairajpuri 1980) Ahmad and Jairajpuri, 1987
= *Enchodelium asaccatum* Dhanachand and Jairajpuri, 1980
= *Actinolaimoides asaccatus* (Dhanachand and Jairajpuri 1980) Siddiqi, 1982
= *Oriverutus lobatus apud* Baqri, 1980, *nec* Siddiqi (1971) [syn. by
Peña-Santiago et al. (2013)]
= *Oriverutus morus* Gambhir et al., 2008 [syn. by
Peña-Santiago et al. (2013)]
O. belloi Liébanas et al., 2011
O. biformis (Loof and Zullini, 2000) comb. nov.
= *Inbionema biforme* Loof and Zullini, 2000
O. costaricensis Liébanas and Peña-Santiago, 2011
O. ecae (Ahmad and Shaheen 2005) Andrassy, 2009
= *Ecanema ecae* Ahmad and Shaheen, 2005
O. hastatus (Siddiqi 1964) Siddiqi, 1971
= *Tylencholaimus hastatus* Siddiqi, 1964
Oriverutus hastulatus Siddiqi, 1971 [syn. by Andrassy (2002)]
O. hastus Ahmad and Jairajpuri, 1982
O. hemihystera Liébanas and Peña-Santiago, 2011
O. istvani Peña-Santiago et al., 2013
O. kalikus Gambhir et al., 2008
O. labiatus Ahmad and Jairajpuri, 1987
O. lobatus Siddiqi, 1971
O. longistylus Ahmad and Jairajpuri, 1987
O. mammillatus (Darekar and Khan 1982) Jairajpuri and Ahmad, 1992
= *Mammillonema mammillatus* Darekar and Khan, 1982
O. masculus Andrassy, 2002
O. maturitatis Andrassy, 1995
O. microdorus Ahmad and Siddiqi, 1997
O. neopagarus Baniyamuddin and Ahmad, 2007
O. nusi Ahmad, 2007
O. occidentalis Peña-Santiago and Peralta, 1995
O. orientalis Andrassy, 2002
O. pagarus Ahmad and Jairajpuri, 1987

- O. papillatus* Ahmad and Siddiqi, 1997
O. parahastus Ahmad and Siddiqi, 1997
O. parangulatus Baqri, 1991
O. parvus Ahmad and Araki, 2002
O. pseudohastus Ahmad and Ahmad, 2002
O. sturhani Ahmad and Shaheen, 2003
O. tropicus Ahmad and Shaheen, 2003
O. vanisti Peña-Santiago et al., 2013

Species transferred to or retained under other genera:

- O. hastatus* (Andrássy 1963) Siddiqi, 1971, to *Malekus* by Andrásy (1995)
 = *Eudorylaimus hastatus* Andrásy, 1963
Enchodorella hastata (Andrássy 1963) Siddiqi, 1964
Longidorella hastata (Andrássy 1963) Jairajpuri and Hooper, 1968
O. impar (Khan and Khan 1964) Siddiqi, 1971, to *Actinolaimoides* by Andrásy (2002)
 = *Longidorella impar* Khan and Khan, 1964 [see Jairajpuri and Ahmad (1992)]
O. ivorensis (Carbonell and Coomans 1982) Ahmad and Siddiqi, 1998, retained in *Paroriverutus* (present paper)
 = *Paroriverutus ivorensis* Carbonell and Coomans, 1982
O. longicaudatus Ahmad and Siddiqi, 1997, to *Paroriverutus* (present paper)
O. macramphidius (Andrássy 1971) Andrásy, 2002, to *Paroriverutus* (present paper)
 = *Drepanodorylaimus macramphidius* Andrásy, 1971

Key to didelphic species

1. Much larger general size: body 1.48–2.21 mm long, odontostyle 38–62 µm long, spicules 69–85 µm long. *biformis*
 Much smaller general size: body up to 1.50 mm long; odontostyle up to 25 µm long, spicules up to 46 µm long 2
2. *Pars refringens vaginae* absent *arcuicaudatus*
Pars refringens vaginae present 3
3. Female tail regularly and perceptibly curved ventrad 4
 Female tail ventrally straight or weakly curved ventrad, dorsally more or less (often visibly) bent dorsad at the end 7
4. Uterus bipartite, its distal portion close the sphincter with special differentiation inside 5
 Uterus simple, lacking any special differentiation..... 6
5. Smaller general size (body 0.87–0.98 mm long); lip region 11–13 µm wide; distal part of uterus bearing small refractive granules; female tail shorter (21–35 µm) *ecae*
 Larger general size (body 0.97–1.35 mm long); lip region 14–15 µm wide; distal part of uterus bearing longitudinal, refractive plications; female tail longer (44–61 µm) *pagarus*¹

6. Larger general size (body 1.11 mm long); odontostyle 18 μm long; tail conical and shorter ($c' = 1.9\text{--}2.2$); spicules 33 μm long *anisi*
 Smaller general size (body 0.79–0.82 mm long); odontostyle 13–14 μm long; female tail subcylindroid and longer ($c' = 3.5\text{--}4.0$); spicules 22 μm long..... *arcuatus*
7. Odontostyle 2.6–3.3 times as long as lip region diameter; female tail 4.0–4.6 anal body diameters long *parahastus*
 Odontostyle up to 2.5 times the lip region width long; female tail less than 3.5 anal body diameters long 8
8. Odontostyle 19 μm long or more 9
 Odontostyle up to 19 μm long 12
9. Lip region 14–15 μm wide; comparatively shorter female tail ($c' = 1.7\text{--}1.8$) *costaricensis*
 Lip region less than 13 μm wide; comparatively longer female tail ($c' > 2.0$) ... 10
10. Smaller general size (body 0.81–0.89 mm long); odontostyle 19–21 μm long or 1.6–1.7 times the lip region width *nusi*
 Larger general size (body 0.92–1.17 mm long); odontostyle 22–25 μm long or 1.9–2.3 times the lip region width..... 11
11. Anterior genital branch visibly less developed than the posterior one; cardia symmetrical; comparatively longer female tail (62–65 μm , $c = 15\text{--}18$, $c' = 3.1\text{--}3.4$)..... *hemihystera*
 Both genital branches equally developed; cardia distinctly asymmetrical, with a dorsal lobe; comparatively shorter female tail (44–54 μm , $c = 20\text{--}22$, $c' = 2.4\text{--}2.6$) *papillatus*
12. Uterus long and complex (tripartite)..... 13
 Uterus short and simple..... 15
13. Larger general size (body 1.30–1.33 mm long); uterus with a long intermediate narrower section *belloi*
 Smaller general size (body less than 1.15 mm long); intermediate section of uterus very short 14
14. Lip region 12–15 μm wide; distal portion of uterus bearing very distinct longitudinal plications; male present *neopagarus*
 Lip region 8–11 μm wide; distal portion of uterus lacking any special differentiation; male absent *tropicus*
15. Body 1.40–1.43 mm long; female tail 5.0–5.1 anal body diameters long *pseudohastus*
 Body up to 1.20 mm long; female tail up to 3.5 anal body diameters long 16
16. Body larger (1.15–1.20 mm long) and very slender ($a = 45\text{--}56$) *mammillatus*²
 Body smaller (up to 1.15 mm long) and less slender ($a < 44$) 17

17. Odontostyle 16–18 μm long or 1.7–1.8 times the lip region width.....*parangulatus*
Odontostyle up to 16 μm long or up to 1.6 times the lip region width..... 18
18. Smaller general size (body 0.65–0.72 mm long); female tail 37–39 μm long *parvus*
Larger general size (body more than 0.80 mm long; female tail more than 40 μm long 19
19. Less slender body ($a = 24\text{--}30$); cardiac glands indistinct or absent
..... *maturitatis*
More slender body ($a > 30$); cardiac glands well developed. 20
20. Odontostyle 12–14 μm long or 1.4–1.6 times the lip region width; more anterior vulva ($V = 49\text{--}50$); male as frequent as female *hastus*
Odontostyle 15–16 μm long or 1.2–1.4 times the lip region width; more posterior vulva ($V = 52\text{--}60$); male absent *labiatus*

Notes on some species

1. Choi et al. (1997) confirmed that *O. pagarus* has a bipartite uterus, a remarkable feature that was not reported in the original description of this species by Ahmad and Jairajpuri (1987).
2. The original description of *O. mammillatus* is not very detailed. It has been herein assumed that *pars refringens vaginae* is present in this species.

Not included in the key

Oriverutus masculus: known only on the base of male specimens.

Additional information on *Oriverutus* didelphic species is provided in Table 1, where a compendium of their main measurements and ratios is presented together with their geographical distribution and the corresponding references. For a key and a compendium of opisthodelphic species, see the recent contribution by Peña-Santiago et al. (2013).

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Table 1. Morphometrics of didelphic species of the genus *Oriverutus* (all measurements in μm , except for L, which is in mm).

Species	n	L	a	b	c	V	c'	lrw	odont.	neck	ph. exp.	abw	pretec	tail	spicul.	ve.sup.	geog. dis.	Ref
<i>O. anisi</i>	1♀	1.11	29	3.8	23	55	1.9	14	18	288			37	48			India, Assam	1
	1♂	1.11	32	3.8	19		2.2		18	292			45	60	33*	6		
<i>O. arcuatus</i>	1♀	0.79	33	3.7	15	50			13–14				40	53			India, Tamil Nadu	2
	1♂	0.82	37	4.0	13								42	62	22	3		
<i>O. arcuicaudatus</i>	3♀♀	0.64–0.71	22–24	3.1–3.3	15.8–19.7	53–55	1.9–2.1	12.0–12.7	16–17	201–216	81–88	18–20	20–31	35–41			Japón	3
	3♂♂	0.61–0.70	25–26	3.0–3.4	16.9–18.7		1.9–2.0	12.7	16–16.5	193–205	74–85	18–20	22–38	36–38	25–27	1		
<i>O. bellai</i>	2♀♀	1.30, 1.33	31, 30	3.5, 3.7	30, 27	55, 50	2.2, 2.5	9.5, 8.5	15.5, 16	369, 356	164, 158	20	59	44, 50			Costa Rica	4
<i>O. biforme</i>	15♀♀	1.53–2.21	22–29	3.5–4.1	38–58	49–56	1.1–1.6		39–66	428–580	38–43%	26–35	69–119	32–56			Costa Rica	5
	5♂♂	1.48–1.87	28–29	3.4–3.9	35–62		0.9–1.3		40–66	402–516		33–35	95–132	29–42	69–85	11–14		
<i>O. costaricensis</i>	2♀♀	1.24, 1.07	26, 24	3.5, 3.8	29, 25	48, 45	1.7, 1.8	14, 15	24	353, 277	179, 125	25, 24	42, 34	43, 42			Costa Rica	6
<i>O. ecae</i>	6♀♀	0.87–0.98	20–25	3.3–3.7	25–38	50–57	0.8–1.0	11–13	19–21	259–283	93–108	25–28	30–45	21–29			Costa Rica	7
	♂	0.89	27	3.3	25		1.3	12	18	256	105	27	63	35	37	11		
	♀	0.82	24	3.4	23	55	1.8	12	20	244	94	20	38	36			Costa Rica	4
<i>O. hastus</i>	6♀♀	0.89–0.93	30–44	3.0–3.8	19–20	49–50	2.3–2.4	8.7*	12–14*	304*	105*	20*	41–53	46–49	–	–	India, Kerala	8
	4♂♂	0.87–1.01	34–42	3.4–3.7	18–23		2–3				37–46%		85–96	42–45	32–33	2		
<i>O. hemithysera</i>	3♀♀	0.92–1.17	27–34	3.3–3.5	15–16	44, 45	3.1–3.4	10–12	22–24	280–330	115–138	19–21	39–65	62–65			Costa Rica	6
<i>O. labiatus</i>	4♀♀	0.87–1.0	31–37	3.4–3.8	21–24	52–60	2.3–2.6	11–13	15–16	253–278	(45–46%)		39–44	41–45	–	–	India, Uttar Pradesh	1
<i>O. mammillatus</i>	3♀♀	1.16–1.20	45–47.5	3.5–4.0	19–20	52–55	3.5*	11.8*	15–17			14		50*	–	–	India, Maharashtra	9
	2♂♂	1.15–1.18	54–56	3.5–3.7	15–16.5	–	3					16		48*	28–30	7		
<i>O. masculus</i>	3♂♂	1.26–1.47	29–31	3.9–4.5	24–30	–	1.8–2.0	14	22–24	305–315				47–53	44–46	10–11	Ecuador	10
<i>O. maturitatis</i>	8♀♀	0.81–0.91	26–28	3.4–3.8	17–20	46–49	2.5–3.3	9.5–10.5	13–14	230–240	105–115	15–16*		45–51*	–	–	Bolivia	11
	2♀♀	0.82–0.92	24–26	3.2–3.8	18–19	46–49	2.5–2.9										Bolivia	10
	1♀	0.96	27	3.4	18	50	3.0											
	1♂	1.04	30	3.5	28	–	1.7							37	38	7	Perú	10
	2♀♀	0.83–1.00	25–26	3.5–3.6	17–21	44–47	2.2–2.5		13–15	245–296				42–52			Ecuador	10

(Continued)

Table 1. (Continued).

<i>O. neopaganus</i>	9♀♀	0.82–1.02	22–27	3.5–4.8	14–18	47–53	2.1–2.5	12–15	16–19	186–263	88–117	20–25	32–41	50–65	30–32	4–6	India, Arunachal Pradesh	12
	6♂♂	0.92–0.99	28–29	3.0–4.0	14–21		2.0–2.7	12–14	16–18	225–304	84–116	21–25	75–83	44–66				
<i>O. mui</i>	11♀♀	0.81–0.89	27–34	3.3–3.6	19–22	44–47	2.1–2.5	11–13	19–21	240–253	97–102	17–19	40–66	40–45	–	–	Singapore	13
<i>O. paganus</i>	3♀♀	0.99–1.22	26–31	3.2–3.9	20–23	48–53	2.2–2.6	14–15	17–19	309–316	(43–47)%	21*	55–66	50–56	–	–	India, Uttar Pradesh	1
	2♂♂	1.11–1.14	31–32	3.6	23	–	1.7–1.8		18–19	306–313			90–93	44–52	36–40	8–9		
	94♀♀	1.14–1.35	28–31	4.1–4.3	19–26	49–55	2.0–3.0	12–13	14–17	274–317	(41–44)%			48–61	–	–	Korea	14
	4♂♂	0.97–1.13	30–31	3.5–4	16–21	–	2.1–2.3		16–18	271–289					33–39	5–6		
<i>O. papillatus</i>	7♀♀	1.10–1.16	34–38	3.2–3.5	20–22	48–50	2.4–2.6	12–13	23–25	325–340	155*	20–22	44–54	51–55	–	–	Fiji Islands (Samoa)	15
<i>O. parahastus</i>	4♀♀	0.71–0.75	24–29	3.5–3.7	10–11	59–60	4.0–4.6	7	18–23	195–209	44–51%	16–17	32–40	65–75	–	–	Colombia	15
<i>O. parangulatus</i>	4♀♀	0.99–1.15	27–38	3.6–3.7	17–22	50–53	2.8–3.0	12–13	17–19	273*	47–50%		38–56	49–60	–	–	India, Sikkim	16
	2♂♂	0.98–1.16	30–32	3.6–3.7	20.5–22	–	2.1–2.3		19				80–88	46–56	34–35	6		
<i>O. parvus</i>	3♀♀	0.65–0.72	20–22	3.2	17–19	54–55	1.8–2.0	10–11	13–14	205–222	81–94	20–21	40–58	37–39			Japan	3
	4♀♀	0.87–0.97	24–27	3.8–4.1	18–21	50–54	2.1–2.4	10–11	15–16	219–254	98–117	20–23	41–51	42–49			Singapore	12
<i>O. pseudohastus</i>	2♀♀	1.40, 1.43	46	3.6, 3.8	15	55, 56	5.0, 5.1	11, 12	18	362, 370	44, 47%	18	62, 84	92, 94			India, Kerala	17
<i>O. tropicus</i>	6♀♀	0.95–1.0	30–32	3.5–3.6	22–24	46–50	2.2–2.8	8–9	15–17	267–284	108–118	16–20	37–58	40–45	–	–	Costa Rica	7
	9♀♀	1.02–1.14	23–33	3.2–4.2	18–22	45–52	2.5–3.0	9–11	16–18	274–320	121–149	17–20	37–57	47–56				4

Notes: 1 – Ahmad and Jairapuri (1987); 2 – Baqri (1980); 3 – Ahmad and Araki (2002); 4 – Liébanas et al. 2011; 5 – Loof and Zullini (2002); 6 – Liébanas and Peña-Santiago (2011); 7 – Ahmad and Shaheen (2005); 8 – Ahmad and Jairapuri (1982). 9 – Dorekar and Khan (1982), 10 – Andrásy (2002); 11 – Andrásy (1995); 12 – Banyamuddin and Ahmad (2007); 13 – Ahmad (2007); 14 – Choi et al. (1997); 15 – Ahmad and Siddiqi (1997); 16 – Baqri (1991); 17 – Ahmad and Ahmad (2002).

n = number of specimens; L = body length; a, b, c, V, c' = Demeanian ratios; lpw = lip region width; odont. = odontostyle length; neck = neck length; ph. exp. = pharyngeal expansion length; abw = anal body width; preec = preectum length; tail = tail length; spicul. = spicule length; ve. sup. = number of ventromedian supplements; geog. dis. = geographical distribution; Ref. = literature reference.

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