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The phylogeny, systematics and fossil record of the Goneplacidae MacLeay (Crustacea, Decapoda, Brachyura) revisited

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Abstract

We review the Gonoplacidae and review the various alternative hypotheses concerning membership within the family. We offer a new cladistic based hypothesis of phylogenetic relationships within the group.

Introduction

Traditionally, the family Goneplacidae MacLeay (Brachyura, Xanthoidea) has been recognized as a monophyletic group (Balss, 1957). Since Guinot (1969a) first suggested that the Goneplacidae was a polyphyletic group, the subfamilial arrangement has been modified by subsequent workers (Guinot, 1969b, 1971, 1978; Manning & Holthuis, 1981; Ng, 1987 and others). In a recent systematic treatment, Lemaitre et al. (2001) have now divided the Goneplacidae into six subfamilies, namely Carcinoplacinae H. Milne Edwards, Chasmocarcininae Serène, Euryplacinae Stimpson, Goneplacinae, Pseudoziinae Alcock, and Trogloplacinae Guinot. Subsequently, Davie (2002) has assigned two additional subfamilies, Pilumnoidinae Guinot & Macpherson and Planopilumninae Serène, to the Goneplacidae, and afforded the Trogloplacinae full family status. Ng & Liao (2002) excluded the Pseudoziinae from the Goneplacidae and elevated the Pseudoziinae to family status, and included the Planopilumninae and Pseudoziinae within the Pseudoziidae.

In a recent paper, we (Karasawa & Kato, in press) provide an adult morphology-based phylogenetic analysis of fourteen genera within the Goneplacidae, based upon forty-five characters, and propose a new classification (Appendix A) and phylogeny of the family. We suggest the division of the Goneplacidae into six subfamilies, viz., Carinocarcinoidinae Karasawa & Kato, Chasmocarcininae, Euryplacinae, Goneplacinae (= Carcinoplacinae), Mathildellinae Karasawa & Kato, and Trogloplacinae. Within the Goneplacidae, the Trogloplacinae and Chasmocarcininae are sister groups nested as the most derived clade, followed by the Carinocarcinoidinae, Goneplacinae, Euryplacinae, and the most basal Mathildellinae. We also suggest the Pseudoziidae is the sister group to the Eriphiidae.

Results

The Goneplacidae *sensu lato* has been commonly recorded from the Paleogene to the Recent and has previously included at least thirty-five fossil genera (Karasawa & Kato, in press). However, distinction between goneplacid on the one hand and panopeid, pilumnid, and pseudorhombilid genera on the other is difficult based solely upon carapace characters (Schweitzer, 2000). A re-examination of fossil taxa previously assigned to the Goneplacidae has shown that sixty-two species, twenty genera, and five subfamilies may be recognized as fossils (Karasawa & Kato, 2002, in press). Sixteen extinct genera previously assigned to the family were not referred to any goneplacid subfamilies and were excluded from the Goneplacidae (Karasawa & Kato, in press). In the same paper, we do not mention the systematic placement of *Bicarinocarcinus* Glaessner

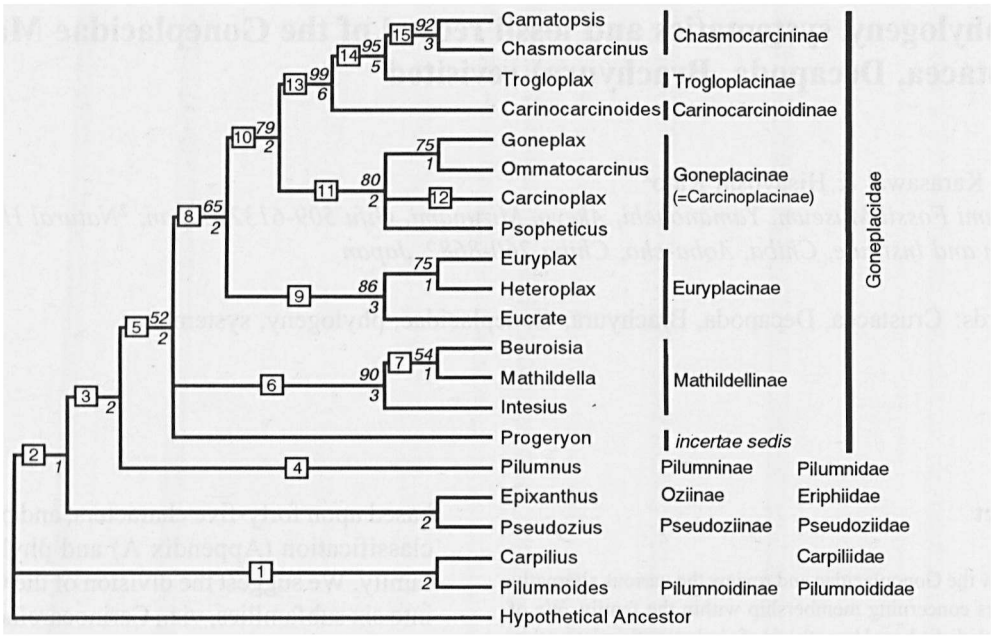

Fig. 1. Strict consensus tree of four most-parsimonious trees of twenty genera; phylogenetic analysis using PAUP* 4.0b (Swofford, 1999), data matrix originating in MacClade version 4.05 (Maddison & Maddison, 2002). This tree is rooted against a hypothetical ancestor. Relative stability of clades was assessed using bootstrap (Felsenstein, 1985) and decay analyses (Bremer, 1994); bootstrapping was based on 100 replicates of random input order. The Bremer support was obtained using constraint trees generated by MacClade and analyzed using PAUP*. Numbers above branches are bootstrap support and numbers below branches are Bremer support. Unambiguous character changes are as follows: box 1 = 45(1); 2 = 23(1), 24(1); 3 = 27(1); 4 = 36(1); 5 = 22(1), 25(1), 46(1); 6 = 38(1), 48(1); 7 = 15(1); 8 = 26(1), 28(1), 43(1); 9 = 16(1); 10 = 4(1); 11 = 1(1), 37(1); 12 = 48(1); 13 = 18(1), 19(1), 20(1), 21(1), 30(1), 32(1); 14 = 12(1), 17(1), 31(1); 15 = 13(1), 48(2).

& Secretan, 1987, which was originally placed within the Carcinoplacinae. The carapace and thoracic sternum characters are most like those of *Carinocarcinoides* Karasawa & Fudouji, the sole genus of the Carinocarcinoidinae. Therefore, *Bicarinocarcinus* is here referred to the Carinocarcinoidinae. Schweitzer et al. (2002) have recently shown that there are close affinities between *Icriocarcinus* Bishop and *Ommatocarcinus* White, and removed the former genus from the Carcinerectidae Beurlen and into the Goneplacidae. This occurrence extends the geologic range for the family back to the Late Cretaceous.

In more recent works, four genera have been added to the Chasmocarcininae. Karasawa & Kato (in press) provisionally transfer *Georgeoplax* Türkay and *Litocheira* Kinaham to the Pilumnidae, following Guinot (1969b, 1971), while Davie (2002) referred both genera to the Chasmocarcininae. They both differ from members of Chasmocarcininae (sensu Karasawa & Kato) in that a wide male abdomen fills the entire space between coxae of pereiopods 5, the thoracic sternite 8 does not possess a supplementary plate, dactyli of pereiopods 5 are not sickle shaped, gonopod 1 is twisted with a distal process, and gonopod 2 is much shorter than gonopod 1. Thus, both genera lack the diagnostic characters of the Chasmocarcininae. Ng (2002) assigned *Acidops* Stimpson and *Parapilumnus* Kossmann to the Chasmocarcininae. However, both genera possess a male abdomen that fills the entire space between coxae of pereiopods 5, have a narrow thoracic sternum with a median sulcus on the anterior part of sternite 4, an anterior margin of the male sterno-abdominal cavity which does not reach the anterior part of sternite 4, short pereiopods 2-5, and dactyli of pereiopods 2-5 terminating with acute chitinous tips. In *Parapilumnus*, the sulcus separating thoracic sternites 6 and 7 is complete (Ng, 2002). These characters are not observed in members of the Chasmocarcininae (sensu Karasawa & Kato) which is why we exclude *Acidops*, *Georgeo-*

plax, *Litocheira* and *Parapilumnus* from the Chasmocarcininae.

Karasawa & Kato (in press) do not discuss the subfamilial placement of *Megaesthesius* Rathbun, *Notonyx* A. Milne Edwards, *Raoulia* Ng, and *Typhlocarcinodes* Alcock, all of which have been excluded from the pilumnid subfamily Rhizopinae Stimpson by Ng (1987). Serène (1964) originally placed *Megaesthesius* within his new subfamily Chasmocarcininae while Davie & Guinot (1996) and Karasawa & Kato (in press) excluded this genus from the subfamily. However, *Megaesthesius* is here reassigned to the Chasmocarcininae based upon male abdomen and thoracic sternum characters. Serène & Soh (1976) assigned *Notonyx* to the Goneplacinae by having a long, elongate gonopod 2 with a long flagellum; we concur. In *Raoulia* and *Typhlocarcinodes*, the male abdominal somites 3-5 are fused, and the male gonopod 2 is long and about equal to gonopod 1 with a long flagellum. Therefore, both genera resemble members of the Trogloplacinae but detailed characters of the male thoracic sternum are not yet known.

In the phylogenetic analysis by Karasawa & Kato (in press), the Pilumnoidinae, assigned to the Goneplacidae by Davie (2002), was not included because Guinot & Macpherson (1987) noted that there is a close relationship between *Pilumnoides* Lucas and *Carpilius* Leach (Carpiliidae Ortmann), as based upon thoracic sternum and cheliped characters. Ng & Guinot (1999) suggested to transfer *Progeryon* Bouvier from the Geryonidae Colosi to the Goneplacidae. Therefore, we have re-examined an adult morphology-based phylogenetic analysis for twenty genera, including *Carpilius*, *Pilumnoides*, and *Progeryon*, based upon 49 morphological characters (Appendix B). Appendix C lists 49 characters and character states used in the present analysis.

The present analysis yielded four most-parsimonious trees, 108 steps long with a consistency index (CI) of 0.6019, a retention index (RI) of 0.7962 and a rescaled consistency index (RC) of 0.4792. A strict consensus of four most-parsimonious trees, indicating bootstrap and Bremer support, is given in Fig. 1. *Pilumnoides*, the sole genus of the Pilumnoidinae, is excluded from the Goneplacidae. *Pilumnoides* and *Carpilius* are sister taxa nested as the most basal clade and both genera share two synapomorphies (10-1, 45-1). D'Udekem d'Acoz (1999) raised the Pilumnoidinae to full family status. The present analysis supports the recognition of the Pilumnoididae and suggests that the family is the sister taxon of the Carpiliidae. The monophyly of the remaining goneplacids is well supported by four synapomorphies (11-1, 22-1, 25-1, 46-1). However, the present analysis is unable to resolve the relationships between *Progeryon* (Goneplacidae incertae sedis) and other goneplacid subfamilies.

Davie (2002) elevated the Trogloplacinae to full family status, although Davie & Guinot (1996) and Karasawa & Kato (in press) pointed out that the Trogloplacinae has close affinities with the Chasmocarcininae. If the Trogloplacinae is treated as a separate family, the remaining goneplacids become a polyphyletic group. D'Udekem d'Acoz (1999) raised the Euryplacinae and Carcinoplacinae to full family status and included both families in the superfamily 'Goneplacoidea'. Stevcic (in Martin & Davis, 2001) also thought to elevate the Euryplacinae to family status. There is a possibility that the six subfamilies defined by Karasawa & Kato (in press) may be raised to full family status, taking into account of these works.

It is not clear which could be a reliable sister group to the Goneplacidae. Guinot (1969b) and Stevcic (in Martin & Davis, 2001) mentioned that there is a close relationship between the Goneplacidae and Geryonidae based upon adult morphology, while Rice (1980) showed that the family is most similar to the Pilumnidae Samouelle based upon zoeal morphology. Von Sternberg & Cumberlidge (2001) suggested that, based upon cladistic and phenetic analyses, the Goneplacidae might be more closely related to the Portunoidea (inclusive of the Geryonidae) than to any family of the Xanthoidea. Karasawa & Kato (in press) show that the Goneplacidae is derived as the sister group to the Pilumnidae.

The subfamilial arrangements of some genera have not yet been satisfactorily cleared. Should the known subfamilies be given full family status? Then, should they be transferred from the superfamily Xanthoidea to the 'Goneplacoidea'? What is a true sister group of the Goneplacidae? These are subjects of forthcoming papers.

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Appendix A. Systematic list of genera currently assigned to the Goneplacidae. Asterisks indicate extinct genus (modified from Karasawa & Kato, in press).

Subfamily Mathildellinae Karasawa & Kato, in press (Paleogene-Recent)

Beuroisia Guinot & Richèr de Forges, 1981, *Branchioplax* Rathbun, 1916*, *Intesius* Guinot & Richèr de Forges, 1981, *Mathildella* Guinot & Richèr de Forges, 1981, *Neopilumnoplax* Serène in Guinot, 1969, *Platypilumnus* Alcock, 1894, *Tehuacana* Stenzel, 1944*

Subfamily Euryplacinae Stimpson, 1871 (Eocene-Recent)

Chlinocephalus Ristori, 1886*, *Corallicarcinus* Müller & Collins, 1991*, *Euryplax* Stimpson, 1859, *Eucrate* de Haan, 1835, *Fravillea* A. Milne Edwards, 1880, *Heteroplax* Stimpson, 1858, *Machaerus* Leach, 1818, *Nancyplax* Lemaitre et al., 2001, *Orbitoplax* Tucker & Feldmann, 1990*, *Psopheticoides* Sakai, 1969, *Stoaplax* Vega et al., 2001*, *Trizocarcinus* Rathbun, 1914

Viaplax Karasawa & Kato, in press*

Subfamily Goneplacinae MacLeay, 1838 (Late Cretaceous-Recent):

Bathyplax A. Milne Edwards, 1880, *Carcinoplax* H. Milne Edwards, 1852, *Goneplax* Leach, 1814, *Icriocarcinus* Bishop, 1988*, *Neommatocarcinus* Takeda & Miyake, 1969, *Notonyx* A. Milne Edwards, 1873, *Ommatocarcinus* White, 1852, *Psopheticus* Wood-Mason, 1892, *Singhaplax* Serène & Soh, 1976

Subfamily Carinocarcinoidinae Karasawa & Kato, in press (Eocene-Oligocene):

Bicarinocarcinus Glaessner & Secretan, 1987*, *Carinocarcinoides* Karasawa & Fudouji, 2000*

Subfamily Trogloplacinae Guinot, 1986 (Recent):

Australocarcinus Davie, 1987, *Trogloplax* Guinot, 1986

Subfamily Chasmocarcininae Serène, 1964 (Eocene-Recent):

Camatopsis Alcock & Anderson, 1899, *Chasmocarcinus* Rathbun, 1898, *Chasmocarcinops* Alcock, 1900, *Collinsius* Karasawa, 1993*, *Falconoplax* van Straelen, 1933*, *Gillcarcinus* Collins & Morris, 1978*, *Hephthopelta* Alcock, 1899, *Megaesthesius* Rathbun, 1909, *Mioplax* Bittner, 1884*, *Orthakrolophos* Schweitzer & Feldmann, 2001*, *Scalopidia* Stimpson, 1858

Goneplacidae incertae sedis (Recent):

Progeryon Bouvier, 1922, *Raoulia* Ng, 1987, *Typhlocarcinodes* Alcock, 1900

Appendix B. Characters and their states used in PAUP* analysis.

1 Front with median notch: present (0), absent (1)
2 Front with median projection: absent (0), present (1)
3 Frontal teeth: present (0), absent (1)
4 Notch between frontal margin and supraorbital angle: distinct (0), indistinct (1)
5 Orbital width: narrow (0), moderate (1), wide (2)
6 Upper orbital fissure: present (0), absent (1)
7 Dorsal region: more or less distinct (0), indistinct (1)
8 Anterolateral teeth: >3 (0), 1-3 (1), 0 (2)
9 Eye stalk: short (0), long (1)
10 Antennular fossae broad laterally: absent (0), present (1)
11 Basal article of antenna reaching front: present (0), absent (1)
12 Ischium longer than merus: long (0), short (1)
13 Merus of maxilliped 3: subquadrate (0), suboval (1)
14 Telson about as long as wide (0), much longer than wide (1)
15 Telson: triangular (0), suboval (1)
16 Somites 4-6 much narrower than 3: absent (0), present (1)
17 Somite 3 much narrower than thoracic sternite 7: absent (0), present (1)
18 Somites 3 and 4: distinct (0), fused (1)
19 Somites 4 and 5: distinct (0), fused (1)
20 Somites 3 and 4: movable (0), immovable (1)
21 Somites 4 and 5: movable (0), immovable (1):
22 Sternum width: narrow (0), wide (1)
23 Sulcus delimiting sternites 4 and 5: complete (0), interrupted medially (1)
24 Sulcus delimiting sternites 5 and 6: complete (0), interrupted medially (1)
25 Sulcus delimiting sternites 6 and 7: complete (0), interrupted medially (1)
26 Sulcus delimiting sternites 7 and 8: complete (0), interrupted medially (1)
27 Median sulcus on sternite 4: present (0), absent (1)
28 Anterior end of sterno-abdominal cavity: posterior on sternite 4 (0), anterior on 4 (1)
29 Prolongation of episternite 7 of male: absent (0), present (1)
30 Sternite 7 laterally covered with sternite 8: absent (0), present (1)
31 Sternite 8 with supplementary plate: absent (0), present (1)
32 Sternite 8 visible ventrally: indistinct (0), distinct (1)
33 Sternite 8 visible posteriorly: indistinct (0), distinct (1)
34 Gonopod 1: stout (0), slender (1)
35 Gonopod 1: slightly sinuous or curved (0), curved (1), sinuous (2)
36 Gonopod 1 with hook-shaped apex: absent (0), present (1)
37 Gonopod 1 with truncated apex: absent (0), present (1)
38 Gonopod 1 strongly inflated proximally: absent (0), present (1)
39 Gonopod 2: long (0), short (1)
40 Flagellum of gonopod 2: long (0), very short (1)
41 Gonopod 2 with wing-like flagellum: absent (0), present (1)
42 Fingers of pereiopods 1 elongate, much longer than palm: absent (0), present (1)
43 Fingers of pereiopods 1 dark in color: present (0), absent (1)
44 Carpus of pereiopods 1 with ventral spine: absent (0), present (1)
45 Basis and ischium of pereiopods 1: distinct (0), indistinct (1)
46 Meri of pereiopods 2-5 length: short (0), long (1)
47 Dactyli of pereiopods 2-5 with corneous tip: present (0), absent (1)
48 Dactyli of pereiopods 5: styliform (0), spatulate (1), sickle-shaped (2)
49 Dactyli of pereiopods 5 with setae: present (0), absent (1)

Appendix C. Input data matrix of forty-nine characters and twenty genera; missing character states indicated by ?

Characters / Taxa	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9
Camatopsis	0 0 1 1 0 1 1 2 0 0 1 1 1 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 1 0 0 1 1 2 0
Chasmocarcinus	0 0 1 1 0 1 1 2 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 1 0 1 1 0 0 1 1 2 0
Trogloplax	0 0 1 1 0 1 1 2 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 1
Carinocarcinoides	0 0 1 1 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 ? 1 1 1 1 0 1 ? ? ? ? ? ? ? ? 1 1 0 0 1 ? ? ?
Carcinoplax	1 0 1 1 1 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 1 0 0 0 1 0 0 0 0 0 01 1 0 1 1 1 0
Goneplax	1 01 1 1 2 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 1 0 0 0 1 0 0 0 0 0 1 01 0 1 1 01 1
Ommatocarcinus	1 1 1 1 2 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 1 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 1
Psopheticus	1 0 1 1 12 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 1 0 0 0 1 0 0 0 0 0 1 1 0 1 1 0 1
Eucrate	0 0 1 0 12 0 1 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 1 0 0 1 1 0 0
Euryplax	0 0 1 0 2 0 1 1 1 0 0 0 0 1 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 1 1 1 0 0 0 1 1 0 0 1 0 0 1 1 0 0
Heteroplax	0 0 1 0 2 0 1 1 1 0 0 0 0 1 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 1 1 1 0 0 0 1 1 0 0 1 0 0 1 1 0 1
Beuroisia	0 0 1 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0 ? ? 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 1 0 1 0
Intesius	0 0 1 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0101010101 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 1 0 1 0
Mathildella	0 0 1 0 1 0 0 0 0 1 1 0 0 0 1 0 0 0 0 01 0 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 1 0 1 0
Progeryon	0 0 1 01 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
Pilumnus	0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 0 0 0 0 1 2 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0
Epixanthus	0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0
Pseudozius	0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0
Carpilius	0 0 1 1 0 1 1 1 0 1 0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 1 0 1 0 1
Pilumnoides	0 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0
Hypothetical Ancestor	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0